

SHORT REVIEW ON BIOLOGY, STRUCTURE, AND MIGRATION OF *THUNNUS ALALUNGA* IN THE INDIAN OCEAN

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SUMMARY

*The most comprehensive contribution to our understanding of albacore tuna, *Thunnus alalunga*, comes from studies in the Pacific and Atlantic Ocean. In the Indian Ocean, there is little information about this species in the literature. In the present paper, we propose a short review on albacore in the Indian Ocean with a particular attention on the biology, the structure, and the migration. We focused on these fields because they are key components of stock assessment undertaken by the Regional Fishery Management Organization. This work is part of an ongoing work on a global review of albacore tuna in the world.*

KEYWORDS: Tuna, Albacore, biology, structure, migration, Indian Ocean, *Thunnus alalunga*.

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1. Introduction

Albacore tuna (*Thunnus alalunga*) is an important commercial species in tropical, subtropical, and temperate pelagic ecosystems (Essington 2003). The species is listed as globally Near Threatened species in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2013) and is recently considered as Vulnerable with high uncertainty in the Indian Ocean (IOTC 2012, 2013). Although albacore tuna has a long history of scientific research and remains the preeminent target species of the commercial tuna fishery, the related literature in the Indian Ocean is scarce in comparison with other oceanic basins like the Atlantic and Pacific Oceans. Furthermore, data on the Indian Ocean tuna fishery may be limited and contain lacuna (Herrera and Pierre 2010), which poses numerous challenges in our understanding of the fishery oceanography of tuna, in particular for tuna albacore (Chen *et al.* 2005). In this context, a comprehensive expertise of our understanding of the Indian Ocean albacore is necessary to adequately address management options and conservation issues. The present review aims at documenting and synthesizing the knowledge on the biology, the structure, and the migration of this species in the Indian Ocean.

2. Materials and methods

Information was collected from various databases (ASFA; PASCAL; Web of Sciences; Elsevier; Springer; Wiley) with the keyword *Thunnus alalunga*. Out of 489 publications rode on overall oceanic regions, we retained (58) publications dealing with the main question on the biology, the structure and the migration of the Indian Ocean albacore tuna. Finally, catches reported by albacore fisheries distribution were mapped from IOTC data (<http://www.iotc.org/data/datasets>) for the Indian Ocean and ICCAT data (<https://www.iccat.int/fr>) for the Atlantic Ocean.

3. Discussion

3.1. Biology

The biology of albacore tuna in the Indian Ocean is not well known and documented. Moreover, there is relatively little new information on albacore stocks in recent years (IOTC 2013). Information on growth, natural mortality, fishing mortality, and length-weight relationship was found in the literature (Table 1). Longevity for this species is currently unknown in the Indian Ocean; it was estimated to reach 13 years in the South Pacific and in the South Atlantic (Lee and Yeh 1993, 2007). Previous studies have estimated that immature (juvenile) albacore are in average 3–5 years old (Suda 1974), with an average weight below 14 kg (Chen *et al.* 2005). Their size distribution in the Eastern Indian Ocean is between 36–128 cm fork length (FL), dominated by sizes between 90 and 115 cm (FL) (Setyadji *et al.* 2012). These lengths are different from those found in the Atlantic and Pacific Oceans where the fisheries target the fish mainly at the surface. Hence, the migrations of juveniles in the Indian Ocean are less documented than in the others oceans. The length at first maturity is estimated at 90 cm (Ueyanagi 1969; Wu and Kuo 1993) with an average weight above 14 kg

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(Chen *et al.* 2005). It is assumed that age at 50% maturity of individuals' albacore is 4-5 years for both sexes (IOTC 2013). Biological parameters and population characteristics of albacore tuna are essential to evaluate as they are main components of appropriate stock assessment and status. These parameters and equations for the Indian Ocean stock are summarized in Table 1. We observed an error in the Weight Length relation used in the working group (Table 1). The correct equation, coming from Penney 1994, is $w = 0.013718 \times L^{3.0973}$. This equation used by IOTC, even corrected, seems not appropriate for the Indian Ocean as the equation comes from a study on southern Atlantic albacore. It could be very interesting to test the others weight-length relation estimated from the Indian Ocean's individuals (Table 1).

Regarding the diet of albacore tuna in Indian Ocean, there is little specific information. Feeding areas are likely located in the Western Indian Ocean off the coast of Somalia and in the Mozambique Channel off the coast of Kenya (Fonteneau 2008; Figure 1). These areas correspond to the upwelling zone, particularly off the Somalia coast (Kaplan *et al.* 2014). In the Western Indian Ocean, albacore mainly feed on *Alepisauridae*, *Polyipnus*, *Carangidae*, *Caproidae*, *Gempylidae*, and *Triacanthidae* (Koga 1958 quoted by Nishida and Tanaka 2004), but also on shrimps, squids and on various cephalopods like octopus (Xu and Tian 2011). Comprehensive studies on the diet of albacore tuna began in the Atlantic by Legendre (1932, 1933, 1934, and 1940), Bouxin and Legendre (1936), Priol (1944), Forest and Ancellin (1947, 1948), and Aloncle and Delaporte (1974a), then in the Pacific by Hugh (1952) and Iversen (1962). The diversity of preys found in the stomach of albacore, in the Atlantic and Pacific Oceans, suggests an opportunistic feeding behavior (example - Salman and Karakulak 2009). In this context, it would be interesting to combine studies on diet of albacore in the Indian Ocean to develop a full comprehensive pattern of albacore feeding.

3.2. Structure and Migration

The Indian Ocean albacore is currently considered as constituting a single stock, its size composition varies with latitude (Hsu 1994). However, based on morphometric and DNA sequences (see Nikolic and Bourjea 2013 for the review), it was hypothesized that two albacore stocks could be present in the Indian Ocean, delimited by the 90°E longitude parallel (Yeh *et al.* 1995). Other genetic data (i.e. Single Nucleotide Polymorphism - SNP) demonstrated a close relationship with the albacore population from the Pacific Ocean (Albaina *et al.* 2013) whereas blood-group frequencies (Arrizabalaga *et al.* 2004) and microsatellites (Montes *et al.* 2012) indicated a relationship with the Atlantic population. Unknown numbers of albacore may also undertake inter-oceanic migrations between the South Atlantic and the South Indian Ocean (Beardsley 1969) as there is no environmental frontier for albacore in the South African waters. Furthermore the occurrence of a genetic homogeneity between the South Atlantic and the West Indian Oceans (Montes *et al.* 2012) is in line with the trans-oceanic hypothesis.

Past genetic studies of immature albacore from the Cape of Good Hope does not reveal any difference in haplotype frequencies with the Atlantic samples (north and south), suggesting that these individuals are originated from the Atlantic Ocean (Chow and Ushima 1995). Koto

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(1969), Hayasi *et al.* (1970), Morita (1977), and Penney *et al.* (1992) proposed that there is a migration of albacore between the Atlantic and Indian Ocean off South Africa coast. The distribution is nearly continuous from Angola, to the Indian Ocean all along the coast of South Africa (Talbot and Penrith 1968). Koto (1969) also suggested a link with the South Pacific, with immigrants within Indian Ocean coming from Pacific Ocean in October to March (spawning season) and emigrants to Indian Ocean from April to September (non-spawning season). In regards to the hypothetical link between these oceans and the heterogeneity inside the Indian Ocean, the single stock hypothesis for the Indian Ocean albacore tuna population is subjected to discussion.

Here, we present a synthetic map (Figure 1) dealing with the distribution and migration of albacore tuna in the Indian Ocean by life stage from the current scientific knowledge (Koto 1969; Suda 1974; Nishikawa *et al.* 1978; Nishikawa *et al.* 1985; Shiohama 1985; Hsu 1994; Yeh *et al.* 1995; Chen *et al.* 2005; Fonteneau 2008).

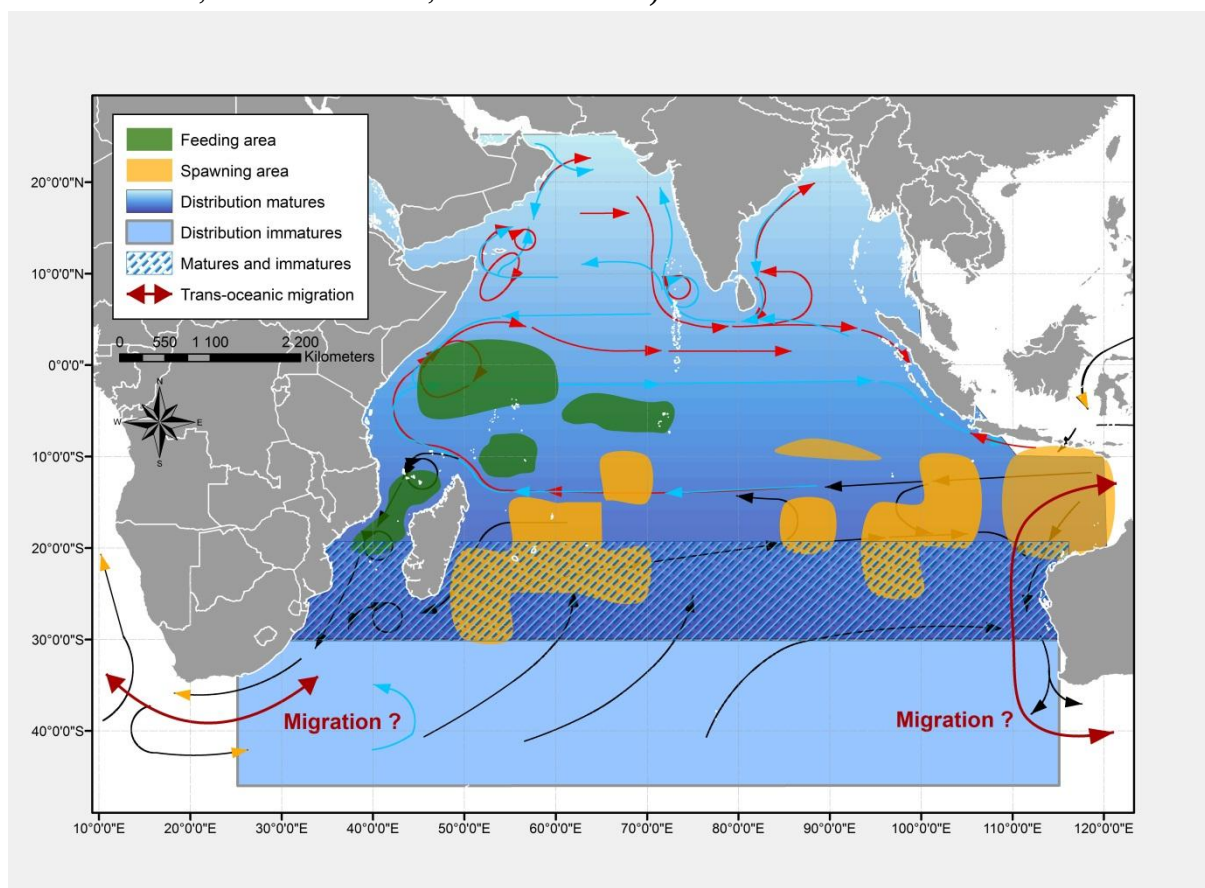


Figure 1: Synthetic map of the distribution of adult and immature albacore in the Indian Ocean and potential migration (red arrow), spawning and feeding areas. Schematic representation of main currents in the Indian Ocean from Schott *et al.* (2009).

We also illustrate immature and mature distribution from available catch-length data from IOTC database (1980 – 2012) in considering two length classes, below and above 90 cm. We present the frequency (Figure 2) and a simple kriging using ARCGIS (software V10.2, ESRI) (Figure 3, Figure 4). Kriging is a geostatistical flexible gridding method that produces visually

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appealing contour and surface plots from irregularly spaced data and demonstrates expression trends suggested by the data set.

Within 10°S and 30°S, the separation of mature, spawning, and immature albacore life history stages is mentioned as coinciding with major oceanic currents in the Indian Ocean (Chen *et al.* 2005) (see in Figure 1). A boundary around 30°S between albacore age groups is suggested (Suda 1974), with spawning albacore in the northern and warmer waters, mature albacore were mainly concentrated between 10°S and 25°S, and immature albacore concentrated south of 30°S (Chen *et al.* 2005). However, the fisheries catches data suggest that this area may drop to 40°S (Figure 2). Likewise, Hsu (1994) distinguished three groups of albacore according to the latitude: mature, spawning and immature groups found respectively northward of 10°S, between 10°S and 30°S, and southward of 30°S. Data on catches of the Taiwanese fishery, which is the major float for albacore in the Indian Ocean, indicate that there is a seasonal North-South migration pattern for both mature and immature albacores (Chen *et al.* 2005). The distribution of catches with all fisheries in Indian Ocean function of the size (immature below 90 cm (FL) and mature above 90 cm) confirmed this separation (Figure 2). The proportion of immature and mature is significantly more important respectively in the south in the north (Figure 2). However, some high spots have been revealed by the Kriging method (Figure 3 and 4). The kriging map for immature is uncompleted and does not fully represent the immature hot spot in the South-West Indian Ocean. This is due to the normalization method giving more weight to the South-East Indian Ocean (Figure 4), as the number of recovery (recursion) per point is higher than in the South-West in the data (see in Figure 6).

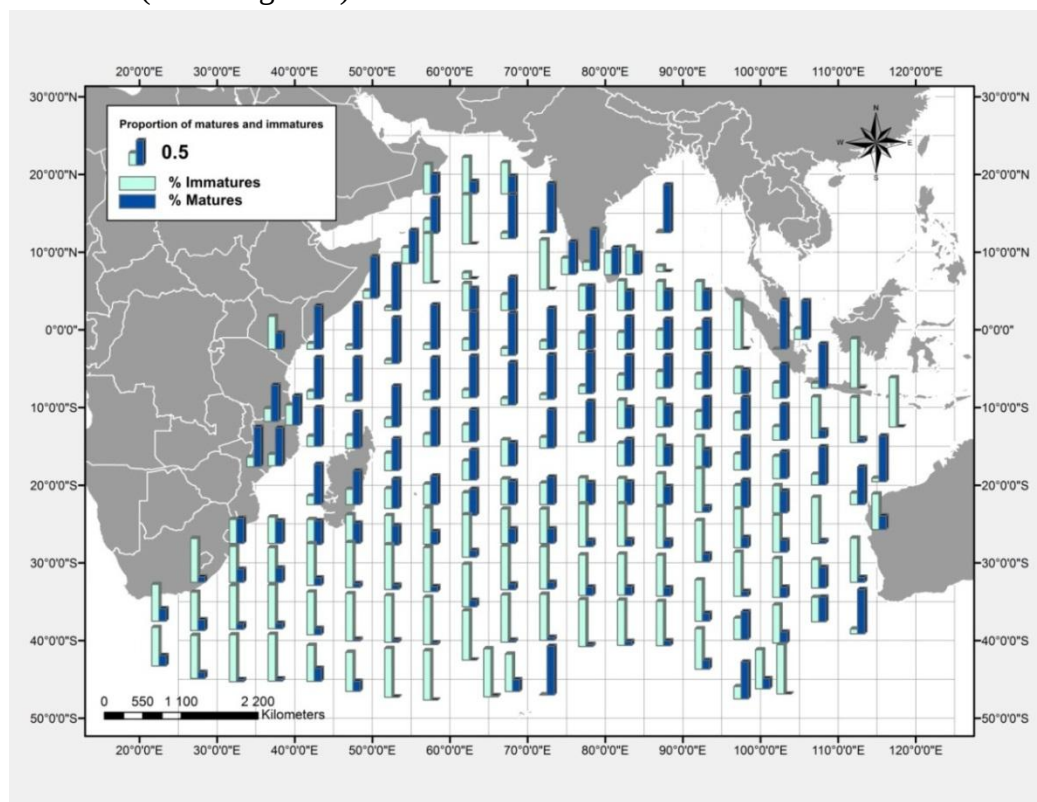


Figure 2: Distribution of mature and immature albacore tuna in the Indian Ocean, all kind of fisheries included from IOTC data between 1980 and 2012.

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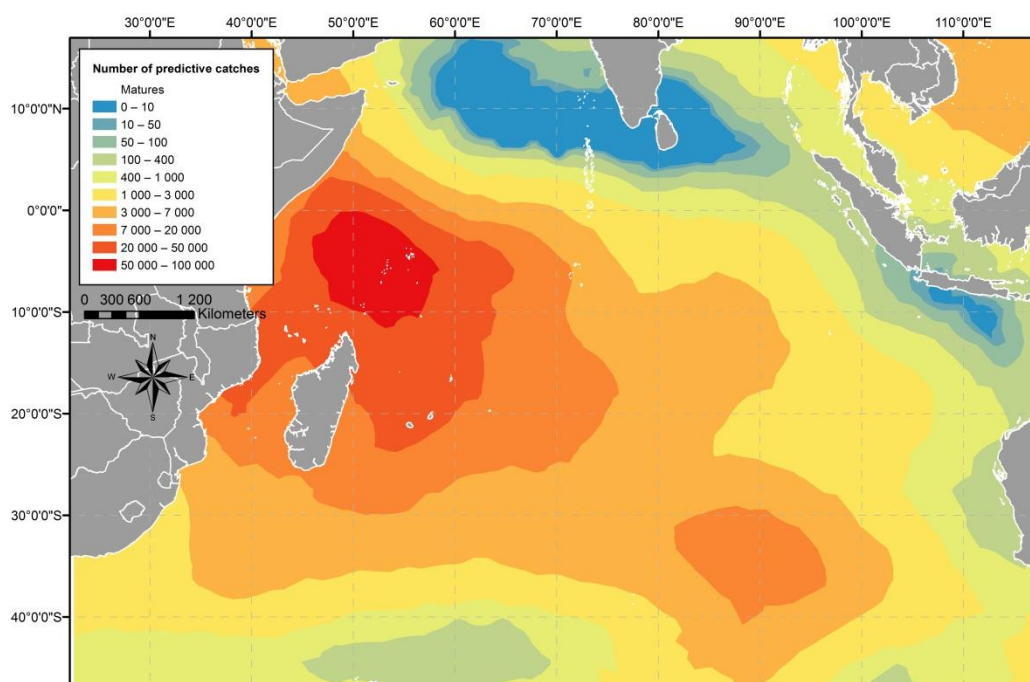


Figure 3: Distribution of matures in the Indian Ocean for all fisheries from IOTC data from 1980 to 2012 with the kriging method.

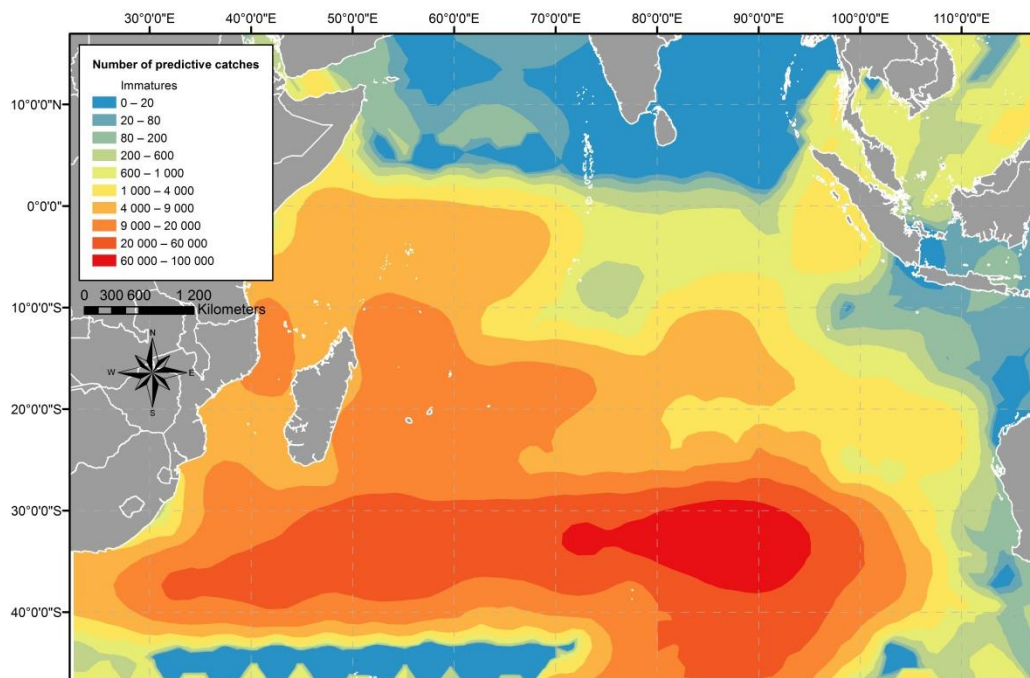


Figure 4: Distribution of immatures in the Indian Ocean for all fisheries from IOTC data from 1980 to 2012 with the kriging method.

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The spawning areas are not well documented in the Indian Ocean but one hypothesis indicates spawning areas between 10°S and 25°S (Ueyanagi 1969), in the Western Indian Ocean, specifically in the waters off eastern Madagascar (Koto 1969; Conand and Richards 1982; Shiohama 1985; Fonteneau 2008; IOTC 2013) (Figure 1). Nishikawa (1985) enlarged this area until 30°S. The larvae of albacore are generally found in warm (superior to 24°C) surface waters (Ueyanagi 1969). The main spawning areas are likely located off the east coast of Madagascar. This is supported by the large quantities of adult albacore concentrated and targeted each year by longline fisheries during the 4th quarter (Figure 5). However, we cannot exclude that the Mozambique Channel is another main spawning area (Figure 2, 3 and 4) during the 3th quarter (Figure 5).

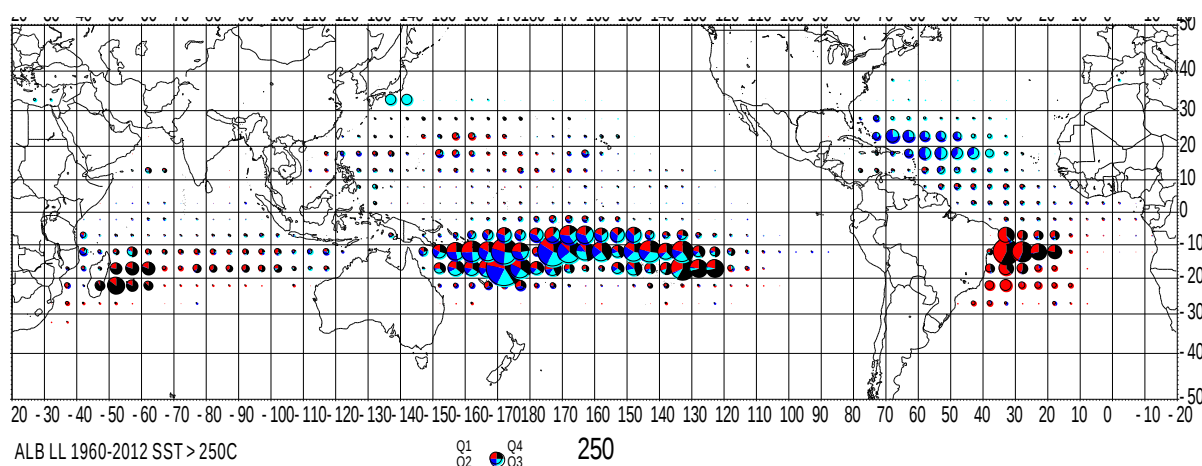


Figure 5: Quarterly albacore catches from 1960 to 2012 by Long Line fishing at Sea Surface Temperature (SST) superior to 25°C.

Moreover, a high density of larvae has also been found in the Cape of Good Hope, around Christmas Island, and North West Australia, (Koto 1969; Nishikawa *et al.* 1978; Nishikawa *et al.* 1985) (Figure 1). Koto (1969) also supposed migratory movements of immature in summer and winter at the Cape of Good Hope in both direction between Atlantic and Indian Ocean (Figure 1). The spawner distributions of albacore is concordant with the hypothesis of others tuna species in the Indian Ocean such as yellowfin and bigeye tuna (Kaplan *et al.* 2014).

Purse-Seine fishing is more superficial than longline (maximum seine depth at 200 m) (Kaplan *et al.* 2014). The distribution of albacore catches as a function of type of fisheries (i.e. PS – Purse-Seine and LL – Long Line) reveals that bigger tuna are caught by the surface fisheries (i.e. PS) in the West Indian Ocean (Figure 6) near the equator, which suggests that this area may be an important spawning zone. The adult at the surface are also found in the Mozambique Channel and in lower proportion in the southeast coast of the Atlantic (Figure 6), re-assuming another suitable spawning area for albacore. The individuals' catches from South Africa are near the Madagascar's coast (Figure 6, Figure 7) and could be a component of the Indian Ocean albacore stock. The surface fisheries reveal also bigger albacore tuna in the South and North-West Atlantic Ocean (Figure 6). The adult albacore found at or near the surface off the coast of Namibia (Figure 6), do they spawn and if so, why is it so far removed

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from other spawning areas supposed in South Atlantic? Do their juveniles remain in the Atlantic? Where do the juveniles migrate to from South Africa? Do these juveniles move then in the Indian Ocean? Many unresolved questions need to be addressed to achieve a sustainable management of stocks of albacore.

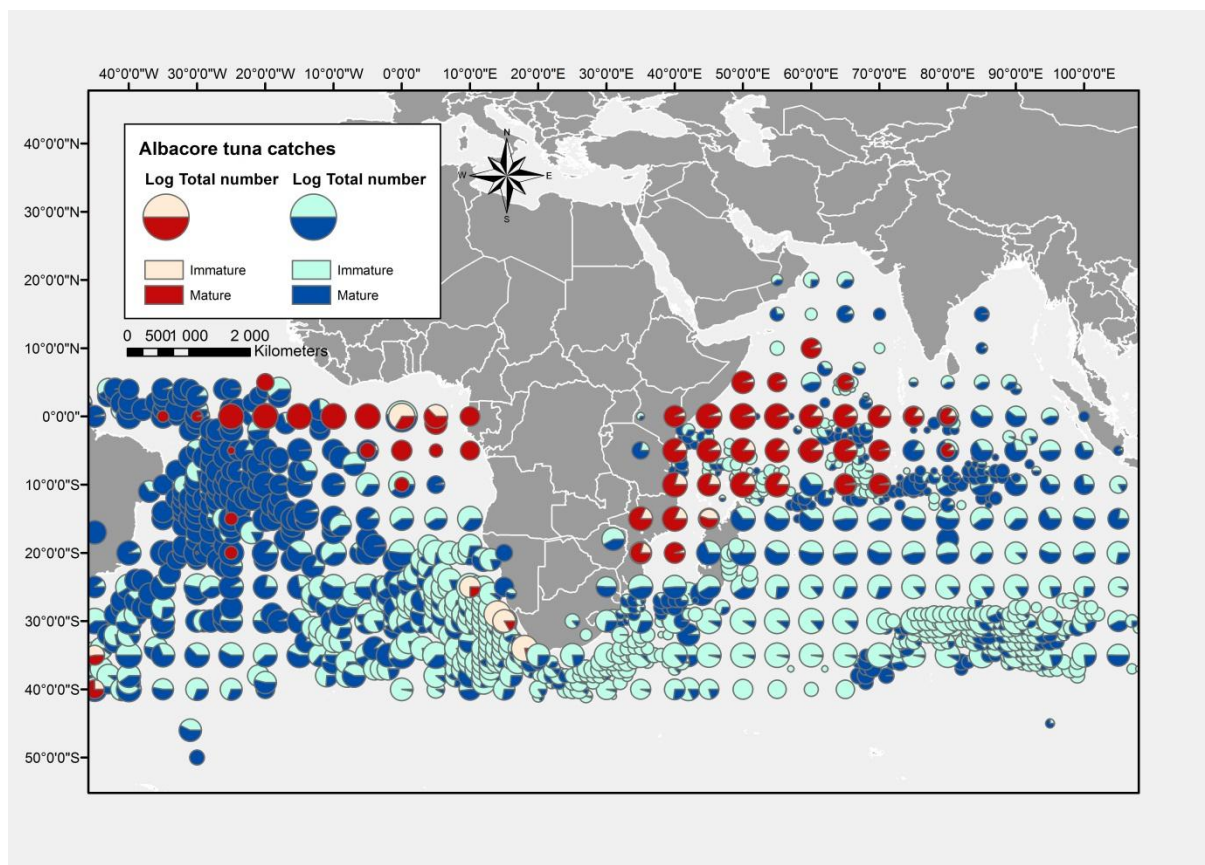


Figure 6: Distribution of proportion between immature (FL inferior to 90 cm) and mature in the Indian and South Atlantic Ocean with Purse-Seine and Longliners from 1980 to 2012 for the Indian Ocean dataset and from 1975 to 2011 for the South Atlantic Ocean dataset. Symbol size varies according to log transformed number of total catches.

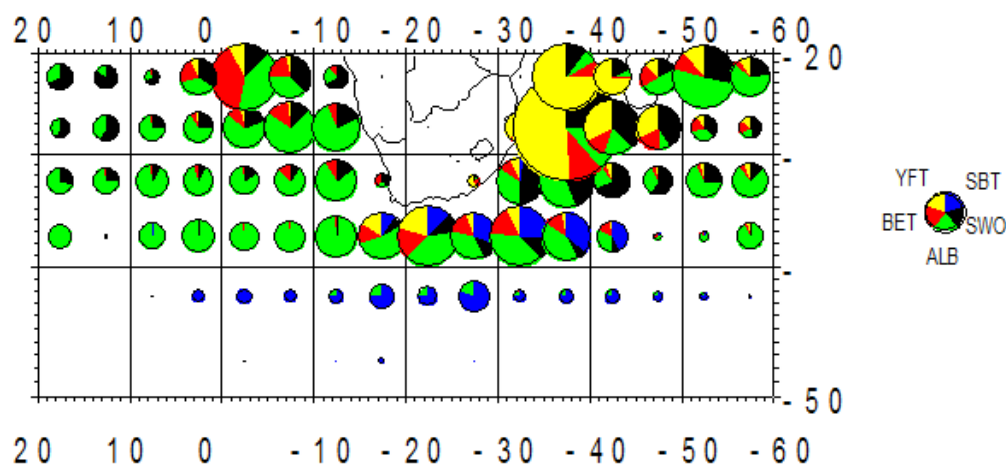


Figure 7. Catches from 2005 to 2012 by Long Line fishing of albacore (ALB), bigeye tuna (BET), yellowfin tuna (YFT), swordfish (SWO), and southern bluefin tuna (SBT) in South Africa.

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4. Conclusion

Understanding stock structure and dynamic of exploited fishes is important for Regional Fisheries Management Organization such as the Indian Ocean Tuna Commission (IOTC), but this assessment is not easy to produce, especially for a migratory species such as the albacore tuna. The migration is a complex issue with numerous external parameters that drive the albacore behavior (environmental components such as suitable temperature window, food availability, oceanic currents) (Sagarmina and Arrizabalaga 2010). Depending on the scientific approach (e.g. serologic, length, genetic), the structure may appear different (Nikolic and Bourjea 2013). For these reasons, it is necessary to use different approaches to adequately and accurately evaluate the stock structure and dynamic over time (e.g. biology, fishery statistics, genetic and chemical markers, otolith shape). In this context, the research managed by Nikolic and Bourjea, the project GERMON (Genetic stRucture and Migration Of albacore tuna), was designed to evaluate spatial and non-spatial management options as recently highlighted by Kaplan *et al.* (2014). The present review illustrates the paucity of information (i.e. low number of publications easily available and the heterogeneity of results) on the structure and the biology of albacore in the Indian Ocean, which highlights the magnitude of the efforts for further studies.

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Weight (W in g)-Fork length (L in cm)		Natural mortality (M)		Fishing mortality (F) Longline		Growth Parameters (L_{∞} = asymptotic length as t approach to ∞ ; k = growth coefficient ; to =theoretical age)	
Equation	Reference	M	Reference	F	Reference		Reference
$w=0.03505 \times L^{2.857}$	Huang et al. 1990	0.2-0.8 (assumed 0.2 before 6 years old, 0.4-0.6 beyond)	Suda 1974	0.07	Suda 1974	$L_{\infty} = 128.127$ cm, $K=0.162$, to = -0.897	Huang et al. 1990
$w=0.032411 \times L^{2.8758}$	Lee and Liu 1992	0.206	Lee et al. 1990	0.24	Lee et al. 1990	$L_{\infty} = 163.71$ cm, $K=0.1019$, to = -2.0668	Lee et al. 1990
$w=0.056907 \times L^{2.7514}$	Hsu 1999; IOTC 2013	0.221	Liu and Lee 1992 by Chang et al. 2001	0.33	Lee and Liu 1992 by Chang et al. 2001	$L_{\infty} = 136$ cm, $K=0.1591$, to = -1.6849	Hsu 1991
$w=0.434 \times L^{2.3428}$	Zhu et al. 2008	0.22-0.25	Chang et al. 1993 by Chang et al. 2001	0.33	Chang et al. 1993 by Pillai and Satheeshkumar 2012	$L_{\infty} = 163.71$ cm, $K=0.1019$, to = -2.0668	Lee and Liu 1992
$w=1 \times L^{2.055}$	Xu and Tian 2011	0.24	Chang et al. 1993 by Pillai and Satheeshkumar 2012			$L_{\infty} = 167.1$ cm, $K=0.097$	Lee and Liu 1992 by Chang et al. 2001
$w=0.08 \times L^{2.7271}$	Setyadji et al. 2012					$L_{\infty} = 123$ cm, $K=0.24$, to = -0.386	Chang and Hsu 1992
$w = 0.013718 \times L^{3.0793}$	IOTC (Equation of Penney 1994 from ICCAT but with an error . The correct equation from original paper, Penney (1994), is $w=0.013718 \times L^{3.0973}$)					$L_{\infty} = 171.4$ cm, $K=0.118$	Chang et al. 1993 by Chang et al. 2001
						$L_{\infty} = 147.2$ cm, $K=0.133$	Chang et al. 1993 by Chang et al. 2001
						$L_{\infty} = 132.2$ cm, $K=0.149$	Chang et al. 2001 (Huang et al. 1990 re-calculated using nonlinear approach by Chang et al. 1993)

Table 1. Biological parameters and population characteristics of Albacore tuna used in the Indian Ocean.

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References

- Albaina A, Iriondo M, Velado I, Laconcha U, Zarraonaindia I, Arrizabalaga H, Pardo MA, Lutcavage M, Grant WS, Estonba A. 2013. Single nucleotide polymorphism discovery in albacore and Atlantic bluefin tuna provides insights into worldwide population structure. *Animal Genetics*, 44(6):678-692
- Aloncle H, Delaporte F. 1974a. Données nouvelles sur le germon *Thunnus alalunga* BONNATERRE 1788 dans le Nord-Est Atlantique. 1ère Partie - Rythmes alimentaires et circadiens. *Revue des Travaux de l'Institut Pêches Maritimes*, 37(4):475-572
- Aloncle H, Delaporte F. 1974b. Données nouvelles sur le germon Atlantique *Thunnus alalunga* Bonnaterre 1788 dans le Nord-Est Atlantique. Deuxième partie. *Revue des Travaux de l'Institut des Pêches Maritimes*, 38(1):9-102
- Arrizabalaga H, Costas E, Juste J, González-Garcás A, Nieto B, López-Rodas V. 2004. Population structure of albacore *Thunnus alalunga* inferred from blood groups and tag-recapture analyses. *Marine Ecology Progress Series*, 282:245-252
- Beardsley G.L. 1969. Proposed Migrations of Albacore, *Thunnus alalunga*, in the Atlantic Ocean. *Transactions of the American Fisheries Society*, 98(4):589-598
- Bouxin J, Legendre R. 1936. La fauna pelagique de l'Atlantique recueillie dans des estomacs de germans au large du golfe de Gascogne -Deuxieme Partie : Cephalopodes. *Annales de l'Institut Océanographique*, Paris, 16(i):1-99, 21
- Chang SK, Hsu CC, Liu HC. 2001. Management implication on Indian Ocean albacore from simple yield analysis incorporating parameter uncertainty. *Fisheries Research* 51:1-10
- Chang SK, Liu HC, Hsu CC. 1993. Estimation of vital parameters for Indian albacore through length-frequency data. *Journal of The Fisheries of Taiwan* 20(1):1-17
- Chang SK, Hsu CC. 1992. Nonlinear estimation on von Bertalanffy growth parameters of Atlantic albacore, *Thunnus alalunga*. *Acta Oceanographica Taiwanica* 29:59-71
- Chen IC, Lee PF, Tzeng WN. 2005. Distribution of albacore (*Thunnus alalunga*) in the Indian Ocean and its relation to environmental factors. *Fisheries Oceanography*, 14:71-80
- Chow S, Ushiyama H. 1995. Global population structure of albacore (*Thunnus alalunga*) inferred by RFLP analysis of the mitochondrial ATPase gene. *Marine Biology*, 123:39-45
- Conand F, Richards WJ. 1982. Distribution of tuna larvae between Madagascar and the Equator, Indian Ocean. *Biological Oceanography*, 1(4):31-336
- Essington TE. 2003. Development and sensitivity analysis of bioenergetics models for Skipjack Tuna and Albacore: A comparison of alternative life histories. *Transactions of the American Fisheries Society*, 132:759-770

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Fonteneau A. 2008. A summarized presentation of the report of the 2nd IOTC WP of the albacore meeting held in Bangkok, November 1st 2008. [Power Point presentation]. IOTC-2008-SC-INF29

Forest J, Ancellin J. 1948-1949. Observations diverses sur *Germo alalunga* G. Rapports de mission présentés à l'Office Scientifique et Technique des Pêches Maritimes

Hayasi S, Koto T, Shin Ghu C, Kume S, Morita Y. 1970. Resources and fisheries of tunas and related fishes in the Atlantic Ocean. Far Seas Fisheries Research Laboratory, 3:18-72

Herrera M, Pierre L. 2010. Status of IOTC databases for tropical tunas. IOTC-2010-WPTT-03. Indian Ocean Tuna Commission, Victoria, Seychelles

Hsu CC. 1991. Parameters estimation of generalized von Bertalanffy growth equation. ACTA Oceanographica Taiwanica, 26:66-77

Hsu CC. 1994. The status of Indian Ocean albacore - A review of previous work. Proceedings of the Fifth Expert Consult on Indian Ocean Tunas. Indo-Pacific Tuna Development and Management Programme. Coll. Vol. Work. Doc. 8:117-124

Hsu CC. 1999. The length-weight relationship of Albacore, *Thunnus alalunga*, from the Indian Ocean. Fisheries Research 41:87-92

Huang CS, Wu CL, Kuo CL, Su WC. 1990. Age and growth of the Indian Ocean albacore, *Thunnus alalunga*, by scales. IPTP Working Paper, FAO IPTP/TWS/90/53:111-122

Hugh Mc. L. 1952. The food of albacore (*Germo alalunga*) of California and Baja California. Bull. Scripps Inst. Océanogr. 6(4):161-172. Berkeley et Los Angeles

Kaplan DM, Chassot E, Amandé JM, Dueri S, Demarcq H, Dagorn L, Fonteneau A. Spatial management of Indian Ocean tropical tuna fisheries: potential and perspectives. 2014. ICES Journal of Marine Science, doi.10.1093/icesjms/fst233

Koga S. 1958. On the stomach contents of tuna in the west Indian Ocean. *Bulletin of the Faculty of Fisheries Nagasaki University* 6:85-92

Koto T. 1969. Studies on the albacore-XIV. Distribution and movement of the albacore in the Indian and the Atlantic Oceans based on the catch statistics of Japanese tuna long-line fishery. Bull Far Seas Fish Res Lab, Japan, 1:115-129 (in Japanese with English abstract)

IOTC. 2012. Report of the Fourth Session of the CTOI Working Party on Temperate Tunas. Shanghai, China, 20-22 August 2012. CTOI-2012-WPTmT04-R[E]:43

IOTC. 2013. Proposition: Résumé exécutive: GERMON. IOTC-2013-SC16-ES01[F]

IUCN (International Union for Conservation of Nature). 2013. IUCN red list of threatened species. Version 2013.1. IUCN, Gland, Switzerland. Available from <http://www.iucnredlist.org> (accessed July 2014)

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Iversen RTB. 1962. Food of albacore tuna, *Thunnus germon* (LACÉPÈDE) in the central and northeastern Pacific. From Fishery bulletin of the Fish and Wildlife Service, 62(214):458-481

Lee YC, Liu HC. 1992. Age determination, by vertebra reading, in Indian albacore, *Thunnus alalunga* (Bonnaterre). Journal of The Fisheries Society of Taiwan, 19(2):89-102

Lee YC, Hsu CC, Chang SK, Liu HC. 1990. Yield per recruit analysis of the Indian Ocean albacore stock. FAO/IPTP/TWS/90/56:14

Lee YC, Yeh SY. 1993. Studies on the ages and growth of South Atlantic Albacore (*Thunnus alalunga*) specimens collected from Taiwanese longliners. Collect Vol Sci Pap ICCAT, 40:354-360

Lee YC, Yeh SY. 2007. Age and growth of South Atlantic albacore – a revision after the revelation of otolith's daily ring counts. Collect Vol Sci Pap ICCAT, 60:443-456

Legendre R. 1940. La faune pélagique de l'Atlantique au large du golfe de Gascogne, recueillie dans les estomacs de germons. Troisième partie, invertébrés (Céphalopodes exclus). Annales de l'Institut Océanographique. Paris, 20(4):127-310

Legendre R. 1934. La faune pélagique de l'Atlantique au large du golfe de Gascogne recueillie dans les estomacs de germons. Première partie, poissons. Annales de l'Institut Océanographique. Paris, 14 (6), p. 249-418, 56 fig.

Legendre R. 1933. La nourriture du germon (*Germo alalunga* Bon.). Ibid., 75, 1931-1933:531-540

Legendre R. 1932. La nourriture du germon (*Germo alalunga*). Archive de Zoologie Expérimentale et Gén. Fasc. 26. t. 74 (vol. jubilaire)

Liu HC, Lee YC. 1992. The yield per recruit analysis for Indian Ocean albacore stock. The Third Asian Fisheries Forum, Singapore, October 26-30, 1992, Asian Fisheries

Montes I, Iriondo M, Manzano C, Arrizabalaga H, Jiménez E, Pardo MA, Goñi N, Davies CA, Estonba A. 2012. Worldwide genetic structure of albacore (*Thunnus alalunga*) revealed by microsatellite DNA markers. Marine Ecology Progress Series, 471:183-191

Morita S. 1977. On the relationship between the albacore stocks of the South Atlantic and Indian Oceans. Collect Vol Sci Pap ICCAT, 7:232–237

Nikolic N, Bourjea J. 2013. Differentiation of albacore stock: review by oceanic regions. ICCAT Recueil de Documents Scientifiques. SCRS/2013/126

Nishida, T, Tanaka M. 2004. General review of Indian Ocean Albacore (*Thunnus alalunga*). IOTC-2004-WPTMT-03:8

Nishikawa Y, Honma M, Ueyanagi S, Kikawa S. 1985. Average distribution of larvae of oceanic species of scombroid fishes, 1956-1981. Far Seas Fisheries Research Laboratory, 12:1-99

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Nishikawa Y, Kikawa S, Honna M, Ueyanagis S. 1978. Distribution atlas of larval tunas, billfislies and related species Results of larval surveys by R/V Shunyo Maru and Shoyo Maru (1956-1975 Far Seas Fisheries Research Laboratory, 9:99

Penney AJ. 1994. Morphometric relationships, annual catches and catch-at-size for south African caught south Atlantic albacore (*Thunnus alalunga*). Coll. Vol. Sci. Pap. ICCAT, 42(1):371-382

Penney AJ, Krohn RG, Wilke CG. 1992. A description of the South African tuna fishery in the southern Atlantic Ocean. Collect. Vol. Sci. Pap. ICCAT, 39:247-259

Pillai NG, Satheeshkumar P. 2012. Biology, fishery, conservation and management of Indian Ocean tuna fisheries. Ocean Sciences Journal. 47(4):411-433

Priol EP. 1944. Observations sur les Germons et les Thons rouges capturés par les pêcheurs bretons. Revue Trav. Off. Sc. Tech. Pêches Maritimes Paris T. XIII. 1944, pp. 387-439

Salman A, Karakulak S. 2009. Cephalopods in the diet of albacore, *Thunnus alalunga*, from the Eastern Mediterranean. Journal of Marine Biology Association of the United Kingdom 89(3):635-640

Schott FA, Xie SP, McCreary JP. 2009. Indian ocean circulation and climate variability. Reviews of Geophysics. 47

Setyadji B, Novianto D, Nugraha B, Sadiyah L. 2012. *Catch and size distribution of albacores (Thunnus alalunga) in the Eastern Indian Ocean*. IOTC-2012-WPTmT04-13

Shiohama T. 1985. Overall fishing intensity and length composition of albacore caught by long line fishery in the Indian Ocean, 1952-1982. IPTP TWS/85/22 91-109

Suda A. 1974. Recent status of resources of tuna exploited by longline fishery in the Indian Ocean. Bulletin of the Fisheries Research Laboratory. 10:27-62

Talbot FH, Penrith, MJ. 1962. Tunnies and marlins of South Africa. Nature, 193:558-559

Ueyanagi S. 1969. Observations on the distribution of tuna larva in the Indo-Pacific Ocean with emphasis on the delineation of spawning areas of albacore, *Thunnus alalunga*. Bulletin / Far Seas Fisheries Research Laboratory, 2:177-219. Xu L, Tian SQ. 2011. A study of fisheries biology for albacore based on Chinese observer data, IOTC-2011-WPTmT03-11

Xu L, Tian SQ. 2011. A study of fisheries biology for albacore based on Chinese observer data, IOTC-2011-WPTmT03-11

Yeh SY, Hui CF, Treng TD, Kuo CL. 1995. Indian Ocean albacore stock structure studies by morphometric and DNA sequence methods. FAO IPTP/TWS/95/2/25

Zhu G, Liuxiong X, Yingqi Z, Dai X. 2008. Length-frequency compositions and weight-length relations for big-eye tuna, yellowfin tuna, and albacore (Perciformes: Scombridae) in

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the Atlantic, Indian, and Eastern Pacific Oceans. *Acta Ichthyologica et Piscatoria*. 38(2):157-161

Wu CL, Kuo CL. 1993. Maturity and fecundity of albacore, *Thunnus alalunga* (Bonnaterre), from the Indian Ocean. *Journal of The Fisheries Society of Taiwan*, 20:135–151

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