

## DIFFERENTIATION OF ALBACORE STOCK: REVIEW BY OCEANIC REGIONS

Natacha Nikolic<sup>1</sup> and Jérôme Bourjea<sup>1</sup>

### SUMMARY

*Because one of the most common problems in fisheries is the definition of management units, we propose in this paper a bibliometric review focusing on the differentiation of Albacore populations, *Thunnus alalunga*, among and within oceanic regions (Atlantic, Pacific and Indian Oceans, and Mediterranean Sea). This paper is the first step of a current work on a global review of Albacore tuna using an international aquatic database (ASFA). For the present purpose, 367 publications—mainly composed of articles (64%), but also conference papers, proceedings and reports (24%), and books (12%)—were analyzed. We will see that the concept of the stock and its delimitation is controversial because of the divergence of results. Such a conclusion makes us believe in the urgent need of further studies targeting this currently overexploited species in most regions of the world, in order to improve management units currently used by regional organizations for fishery management.*

### RÉSUMÉ

*Parce que l'un des problèmes les plus récurrents en halieutique est la définition même des unités de gestion, nous proposons dans ce papier un aperçu bibliographique traitant de la différenciation des populations de thon germon, *Thunnus alalunga*, au sein et entre les régions océaniques (l'océan Atlantique, Pacifique et Indien, et la mer Méditerranée). Ce papier est la première étape d'une revue en cours de rédaction sur le thon germon dans laquelle nous avons utilisé une base de données internationale aquatique (ASFA). Un total de 367 publications ont été traité comprenant principalement des articles scientifiques (64%), puis des conférences et rapports (24%), et des ouvrages (12%). Nous verrons que la notion de stock pour cette espèce et leur délimitation sont ambiguës du fait des résultats divergents des études et de leur nature. Le principal constat est le besoin immédiat de travaux supplémentaires sur cette espèce considérée surexploitée dans la plupart des régions du monde et qui permettrait d'améliorer les limites des unités de stock actuellement utilisées par les organisations régionales des pêches.*

### KEYWORDS

*Albacore, stock, structure, distribution, *Thunnus alalunga**

<sup>1</sup> IFREMER, Institut Français de recherche pour l'Exploitation de la Mer, Délégation Océan Indien, La Réunion,  
E-mail: natacha.nikolic@ifremer.fr

## **I. Introduction**

The management and conservation of Albacore are under the jurisdiction of several international management organizations (commissions) such as ICCAT (International Commission for the Conservation of Atlantic Tunas), IOTC (Indian Ocean Tuna Commission), WCPFC (West and Central Pacific Fisheries Commission)/ Secretariat of the Pacific Community-Ocean Fisheries Programme (SPC-OFC), and IATTC (Inter American Tropical Tuna Commission), which is one of the RFMOs (Tuna Regional Fisheries Management Organizations) tasked with the sustainable management of fishery resources.

These commissions manage albacore with a six-stock model, which includes the Mediterranean Sea, North Atlantic, South Atlantic, Indian Ocean, North Pacific Ocean and South Pacific Ocean. However, these stocks are controversial because of the limited understanding of spawning areas, the geographic distribution of fisheries, life-history variables, the results of tagging (Arrizabalaga *et al.* 2002, 2003, 2004) and genetic studies (Davies *et al.* 2012 ; Montes *et al.* 2012 ; Albaina *et al.* 2013).

In this paper, we discuss the potential population structure by stock using the international database Aquatic Sciences and Fisheries Abstract (ASFA) by CSA that dates from 1955 to May 2013. Overwhelmingly cited by a majority of aquatic science librarians as their primary database, the ASFA series is the premier reference in the field of aquatic resources. Input to ASFA is provided by a growing international network that monitors serial publications (articles, books, reports and conferences). However, some of the major publications are not in the database and hence not included in this paper, and we apologize for that.

This bibliometric review allows discussion about the management units and stock definitions. Stock identification is an integral component of modern fisheries stock assessments, and in turn, of effective fisheries and endangered species management (Begg *et al.* 1999). However, considering the importance of identifying the stock structure of a species, it is surprising that there is a scarcity of implemented stock identification requirements, a point already raised by Begg *et al.* (1999).

## **II. Differentiation among oceanic regions**

The differentiation (or heterogeneity) among the four oceanic regions (Atlantic, Pacific and Indian Oceans, and Mediterranean Sea) is highlighted by the majority of publications (Table 1). The differentiation among the regions' management of albacore stocks with a six-stock model (Mediterranean Sea, North Atlantic, South Atlantic, Indian Ocean, North Pacific Ocean and South Pacific Ocean) is consistent with bibliometric analysis. Nonetheless, the next chapter reveals that the differentiation within the regions' management of albacore with a six-stock model, particularly the differentiation within the management unit (the six stocks already defined), is inconsistent with the findings of a majority of publications.

**Table 1.** Publications dealing with the differentiation among the oceanic regions of albacore. Blue indicates that the publication is consistent with the management unit defined. Red indicates that the publication is not consistent with the management unit defined.

| Oceanic Regions          | Differentiation |                     | Reference                      | Method   | Conclusions   | Consistent with management unit |    |
|--------------------------|-----------------|---------------------|--------------------------------|--|---|---------------------------------|----|
|                          | Yes             | No                  |                                |  |   | Yes                             | No |
| Atlantic - Mediterranean | x               |                     | Keyvanfar 1962                 | Serologic, proteomic   | Difference between and within Atlantic and Mediterranean albacore   | x                               |    |
|                          | x               |                     | De Metro et al. 1997           | Tagging  | Low migration between Mediterranean and Atlantic  | x                               |    |
|                          | x               |                     | Ortiz and Cort 1998            | Tagging  | Low migration between Mediterranean and Atlantic  | x                               |    |
|                          |                 | x                   | Viñas et al. 1999              | Genetic  | No differences between albacores from the Mediterranean Sea and those from the Atlantic   |                                 | x  |
|                          |                 | x                   | Pujolar et al. 2003            | Genetic  | No genetic heterogeneity was observed between Mediterranean and Azores (East Atlantic) samples  |                                 | x  |
|                          | x               |                     | Arrizabalaga et al. 2002, 2003 | Tagging  | Low migration between Mediterranean and Atlantic  | x                               |    |
|                          | x               |                     | Arrizabalaga et al. 2004       | Lectins in blood groups  | Mediterranean and North Atlantic populations are distant  | x                               |    |
|                          | x               |                     | Viñas et al. 2004              | Genetic  | Differentiation between NE Atlantic and Mediterranean   | x                               |    |
|                          | x               |                     | Nakadate et al. 2005           | Genetic  | Strong frequency differences between Atlantic and Mediterranean samples. Low gene flow between Mediterranean and Atlantic   | x                               |    |
|                          | x               |                     | Goni et al. 2011               | Diet, Isotope  | High difference between Mediterranean and Northeast Atlantic  | x                               |    |
|                          | x               |                     | Mele et al. 2010               | Parasites  | Differentiation between NE Atlantic and Mediterranean   | x                               |    |
|                          | x               |                     | ICCAT 2011                     | Tagging  | The exchange between the Atlantic and Mediterranean is minor  | x                               |    |
|                          | x               |                     | Davies et al. 2011             | Genetic  | NE Atlantic and Mediterranean are strongly differentiated   | x                               |    |
|                          | x               |                     | Montes et al. 2012             | Genetic  | Distinguished the Mediterranean Sea population from the rest  | x                               |    |
| x                        |                 | Albaina et al. 2013 | Genetic                        | Significant heterogeneity between Atlantic (NE, NW, IRE, SE) and Mediterranean | x   |                                 |    |
| Atlantic - Indian        | x               |                     | Suzuki 1962                    | Serologic  | Indian Ocean albacore were significantly different from those of the Atlantic and Pacific, but were most similar to those of the Pacific                            | x                               |    |
|                          | x               |                     | Koto 1969                      | Catch, Length  | Difference between Atlantic and Eastern Indian samples  | x                               |    |
|                          | x               |                     | Yeh et al. 1995                | Morphometric, Genetic  | Possible 2 stocks: south Atlantic and Indian  | x                               |    |
|                          | x               |                     | Yeh et al. 1997                | Genetic  | South Atlantic differs of East Indian   | x                               |    |
|                          | x               |                     | Zhu et al. 2008                | Length   | Differences North Atlantic and West Indian  | x                               |    |
|                          |                 | x                   | Montes et al. 2012             | Genetic  | Homogeneity between South Atlantic and Indian Oceans  |                                 | x  |
|                          | x               |                     | Albaina et al. 2013            | Genetic  | Significant heterogeneity between oceans but albacore from the Indian Ocean were most divergent from the Atlantic and Mediterranean than from Pacific Ocean samples | x                               |    |

|                                |   |   |                       |                                      |   |   |   |
|--------------------------------|---|---|-----------------------|--------------------------------------|---|---|---|
| <b>Atlantic - Pacific</b>      | x |   | Suzuki 1962           | Serologic                            | Highly significant difference in the antigen frequencies between the Atlantic and Pacific albacore  | x |   |
|                                |   | x | Graves and Dizon 1989 | Genetic                              | The two groups had either been separated for a short period of time in evolutionary terms   |   | x |
|                                | x |   | Chow and Ushiana 1995 | Genetic                              | Highly significant heterogeneity was evident among Atlantic and Pacific   | x |   |
|                                | x |   | Takagi et al. 2001    | Genetic                              | Differentiation within and between the Pacific and Atlantic   | x |   |
|                                | x |   | Zhu et al. 2008       | Length                               | Differences North Atlantic and Southeast Pacific  | x |   |
|                                | x |   | Davies et al. 2011    | Genetic                              | NE Atlantic and SW Pacific are strongly differentiated  | x |   |
|                                | x |   | Albaina et al. 2013   | Genetic                              | Significant heterogeneity between oceans  | x |   |
| <b>Pacific - Indian</b>        | x |   | Suzuki 1962           | Serologic                            | Indian Ocean albacore were significantly different from those of the Atlantic and Pacific, but were most similar to those of the Pacific                            | x |   |
|                                | x |   | Lewis 1990            | review: Catch, Morphometric, Tagging | Limited interchange   | x |   |
|                                | x |   | Chow and Kishino 1995 | Genetic                              | Differentiation between Indo-Pacific albacore   | x |   |
|                                | x |   | Zhu et al. 2008       | Length                               | Differences West Indian and Southeast Pacific   | x |   |
|                                | x |   | Montes et al. 2012    | Genetic                              | Differentiation between Pacific and Indian albacore   | x |   |
|                                | x |   | Albaina et al. 2013   | Genetic                              | Significant heterogeneity between oceans but Indian Ocean albacore were differentiated to a small degree from Pacific Ocean albacore                                | x |   |
| <b>Pacific - Mediterranean</b> | x |   | Davies et al. 2011    | Genetic                              | Mediterranean and SW Pacific are strongly differentiated  | x |   |
|                                | x |   | Montes et al. 2012    | Genetic                              | Distinguished the Mediterranean Sea population from the rest  | x |   |
| <b>Indian - Mediterranean</b>  | x |   | Montes et al. 2012    | Genetic                              | Distinguished the Mediterranean Sea population from the rest  | x |   |
|                                | x |   | Albaina et al. 2013   | Genetic                              | Significant heterogeneity between oceans but albacore from the Indian Ocean were most divergent from the Atlantic and Mediterranean than from Pacific Ocean samples | x |   |

### III. Differentiation within oceanic regions

The differentiation within the four oceanic regions (Atlantic, Pacific and Indian Oceans, and Mediterranean Sea) can be divided in two categories, i) between the North and South, ii) within management units which concern the differentiation within the north or the south except for the Mediterranean Sea and Indian Ocean (Table 2). The differentiation between the North and South (i) of Atlantic and Pacific is show by the greater part of publications and is in agreement with the management units take into account by the Commissions (Table 2). Concerning the differentiation within management units (ii) while sub-stocks are proposed by most of the scientific work (Table 2), they are not considered as separate units.

**Table 2.** Publications deal with the differentiation within the oceanic regions and management units of albacore. Blue, the publication is consistent with the management unit defined. Red the publication is not consistent with the management unit defined.

| Oceanic Region | Differentiation area | Differentiation         |                     | Reference                  | Method   | Conclusions  | Consistent with management unit                            |    |   |
|----------------|----------------------|-------------------------|---------------------|----------------------------|--|--|--|----|---|
|                |                      | Yes                     | No                  |                            |  |  | Yes  | No |   |
| Atlantic       | North - South        | x                       |                     | Beardsley 1969             | Catch  | Two spawning areas (western North and South Atlantic)  | x  |    |   |
|                |                      | x                       |                     | Koto 1969                  | Catch, Length  | Difference distribution of length class. Two spawning areas (North and south)                              | x  |    |   |
|                |                      | x                       |                     | Hayasi et al. 1970         | Length   | Difference distribution of length class  | x  |    |   |
|                |                      | x                       |                     | Ueyanagi 1971              | Catch Larvae   | Two spawning areas (north and south)   | x  |    |   |
|                |                      | x                       |                     | Shiohama 1971, 1973, 1974  | Catch  | Difference north and south   | x  |    |   |
|                |                      | x                       |                     | Uozumi 1996                | Catch  | Difference north and south   | x  |    |   |
|                |                      |                         | x                   | Chow and Ushiyama 1995     | Genetic  | No heterogeneity between North and South   |  | x  |   |
|                |                      | x                       |                     | Ortiz and Cort 1998        | Tagging  | No mixing between north and south  | x  |    |   |
|                |                      | x                       |                     | Takagi et al. 2001         | Genetic  | Differences between the 2 Atlantic hemisphere samples (NEA and SWA)  | x  |    |   |
|                |                      | x                       |                     | Arrizabalaga et al. 2002   | Tagging  | No albacore released in the North Atlantic or the Mediterranean has been recaptured in the South Atlantic. | x  |    |   |
|                |                      |                         | x                   | Nakadate et al. 2005       | Genetic  | Differences significant between the samples from the Atlantic (NEA and SWA)                                |  | x  |   |
|                |                      |                         | x                   | Montes et al. 2012         | Genetic  | However the samples of Bay of Biscay was nearest of the South Atlantic than the North (Ireland) samples.   |  | x  |   |
|                |                      | x                       | Albaina et al. 2013 | Genetic                    | No differences between northern and southern populations |  | x  |    |   |
|                |                      | Within management units | x                   |                            | Serene 1969  | Serum esterase   | Heterogeneities in the Northeast with different phenotypes |    | x |
|                |                      |                         | x                   |                            | Hallaire and Dao 1971                                    | Serum esterase   | Heterogeneities in the Northeast                           |    | x |
|                | x                    |                         |                     | Aloncle and Delaporte 1974 | Tagging, Color and size of fishes, Parasites             | 3 populations across the NEA   |  | x  |   |

|               |                         |                     |         |                                |                                |   |   |   |
|---------------|-------------------------|---------------------|---------|--------------------------------|--------------------------------|---|---|---|
|               |                         | x                   |         | Aloncle and Delaporte 1979     | Tagging, Length                | Heterogeneities in the Northeast with difference between the Bay of Biscay and Azores   |   | x |
|               |                         | x                   |         | Hue 1980a                      | Tagging                        | Heterogeneities in the North population. Migration toward south during the winter and north during the summer                             |   | x |
|               |                         | x                   |         | Hue 1979, 1980b                | Electrophoresis, Tagging       | 2 groups in the north east Atlantic   |   | x |
|               |                         | x                   |         | Bard 1981                      | Catch, Tagging                 | Consistent with Aloncle and Delaporte 1974  |   | x |
|               |                         | x                   |         | Bard 1982                      | Catch                          | 2 spawning areas in the South Atlantic (west and central)   |   | x |
|               |                         | x                   |         | Ortiz and Cort 1998            | Tagging                        | Results consistent with Aloncle and Delaporte 1974 (migration)  |   | x |
|               |                         | x                   |         | Takagi et al. 2001             | Genetic                        | NE Atlantic sample was significantly heterogeneous  |   | x |
|               |                         | x                   |         | Davies et al. 2011             | Genetic                        | 3 populations across the NEA  |   | x |
|               |                         | x                   |         | Chand and Yeh 2012             | Catch                          | South Atlantic in 3 sub-areas   |   |   |
|               |                         |                     | x       | Albaina et al. 2013            | Genetic                        | No within-ocean heterogeneity   | x |   |
| Mediterranean | Within management units | x                   |         | Keyvanfar 1962                 | Serologic, proteomic           | Difference between Mediterranean albacore groups  |   | x |
|               |                         | x                   |         | Aloncle and Delaporte 1976     | Tagging                        | Possible entrance of individuals from the North Atlantic to the Mediterranean   |   | x |
|               |                         | x                   |         | Aloncle et al. 1976            | Tagging                        | Possible entrance of individuals from the North Atlantic to the Mediterranean   |   | x |
|               |                         | x                   |         | Arena 1978                     | Morphometric                   | Different growth rates and age of maturity  |   | x |
|               |                         | x                   |         | Dicinta and Piccinetti 1978    | Catch larvae                   | Independent spawning area existing in the western Mediterranean   |   | x |
|               |                         |                     | x       | Pujolar et al. 2003            | Genetic                        | No genetic heterogeneity was observed within Mediterranean samples  | x |   |
|               |                         |                     | x       | Nakadate et al. 2005           | Genetic                        | No significant heterogeneity between central and east   | x |   |
|               |                         | x                   |         | Goni et al. 2011               | Diet, Isotope                  | Consistent with the existence of separate spawning grounds in the Tyrrhenian Sea and in the South Adriatic Sea                            |   | x |
|               |                         | x                   |         | Davies et al. 2011             | Genetic                        | 2 populations East and West   |   | x |
|               |                         | x                   |         | Montes et al. 2012             | Genetic                        | 2 populations East and West : Tyrrhenian and Adriatic Sea samples were grouped together and could be differentiated from the Balearic Sea |   | x |
|               | x                       | Albaina et al. 2013 | Genetic | No heterogeneity within-ocean  | x                              |   |   |   |
| Pacific       | North - South           | x                   |         | Kurogane and Hiyama 1958, 1959 | Morphometric                   | Differences in morphometry between North and South  | x |   |
|               |                         | x                   |         | Otsu and Ushida 1963           | Tagging, morphometric          | North Pacific is an unique stock  | x |   |
|               |                         | x                   |         | Ishii 1965                     | Morphometric                   | Differences in morphometry between North and South  | x |   |
|               |                         | x                   |         | Nakamura 1969                  | Morphometric, Catch statistics | Differences North and South with probably negligible migration  | x |   |

|   |                         |        |                         |                                      |  |  |              |  |
|---|-------------------------|--------|-------------------------|--------------------------------------|--|--|--------------|--|
|   |                         | x      | Lewis 1990              | review: Catch, Morphometric, Tagging | Negligible migration of albacore across the equator in the Pacific. Two spawning areas separated (North and South) | x  |              |  |
|   |                         |        | x                       | Chow and Ushima 1995                 | Genetic  | No heterogeneity between North and South   |              | x  |
|   |                         | x      |                         | Takagi et al. 2001                   | Genetic  | Differences between the 2 Pacific hemisphere samples. Each one has a large spawning group from west to mid tropical    | x            |  |
|   |                         |        | x                       | Montes et al. 2012                   | Genetic  | No differences between North and South Pacific   |              | x  |
|   |                         | x      |                         | Aranda et al. 2010                   | Tagging  | Separation north and south   | x            |  |
|   |                         |        | x                       | Albaina et al. 2013                  | Genetic  | No differences between northern and southern populations   |              | x  |
|   | Within management units | x      |                         | Godsil 1948                          | Morphometric   | Morphometric differences between western and eastern Pacific   |              | x  |
|   |                         |        | x                       | US. HO 1948                          | Fisheries  | Rapid migration from the east into the West Coast  | x            |  |
|   |                         |        | x                       | Clemens 1961                         | Tagging  | Migration between the American mainland and the Hawaiian Islands and Japan   | x            |  |
|   |                         | x      |                         | Laur and Lynn 1977                   | Tagging, Length  | Evidence that the shoreward-migrating albacore of the Pacific Northwest and California are independent groups          |              | x  |
|   |                         | x      |                         | Laur and Nishimoto 1979              | Tagging  | Two substocks constitute the North with different migratory patterns   |              | x  |
|   |                         | x      |                         | Laur and Wetherall 1981              | Tagging, morphometric  | Different growth rates and length frequency in two groups of North Pacific   |              | x  |
|   |                         | x      |                         | Laur 1983                            | Tagging  | Two substocks in the North Pacific.  |              | x  |
|   |                         | x      |                         | Lewis 1990                           | review: Catch, Morphometric, Tagging   | Existence of two groups of albacore in the North Pacific   |              | x  |
|   |                         | x      |                         | Takagi et al. 2001                   | Genetic  | Differences between Southwest and Southeast Pacific  |              | x  |
|   |                         | x      |                         | Montes et al. 2012                   | Genetic  | 2 populations in the south: East and West  |              | x  |
|   |                         | x      |                         | Williams et al. 2012                 | Length   | Variation in length-at age and growth parameters across longitudes in South Atlantic from west to central              |              | x  |
|   |                         | x      |                         | Farley et al. 2013                   | Morphometric   | Albacore in easterly longitudes on average having heavier gonads for their size than fish further west (South Pacific) |              | x  |
|   |                         |        | x                       | Albaina et al. 2013                  | Genetic  | No within-ocean heterogeneity  | x            |  |
|   |                         | Indian | Within management units | x                                    |  | Suda 1974  | Morphometric | Boundary at about 30°S between albacore age groups |
| x |                         |        |                         | Hsu 1994                             | Catch, Morphometric  | Size composition varies with latitude  |              | x  |
| x |                         |        |                         | Yeh et al. 1995                      | Genetic, Morphometric  | Possible two stocks delimited by the 90°E longitude  |              | x  |
| x |                         |        |                         | Yeh et al. 1997                      | Genetic  | The variation between group is higher than within group  |              | x  |
| x |                         |        |                         | Nishikawa et al. 1985                | Catch larvae   | Two spawning areas, in the east (near Madagascar) and the west side  |              | x  |
|   | x                       |        |                         | Albaina et al. 2013                  | Genetic  | No within-ocean heterogeneity  | x            |  |

#### IV. Discussion

All oceans have probably some sub-populations because few fish species form single, panmictic populations throughout their geographic range (Metcalf 2006). Supplemental investigations are recommended to highlight the heterogeneity of the stock. The currently accepted definition of a stock is a population unit assumed to be homogeneous for particular management purposes (Begg and Waldman 1999), meaning a population or sub-population in which intrinsic parameters (growth, recruitment, mortality and fishing mortality) are the significant factors in determining population dynamics, while extrinsic factors (immigration and emigration) are insignificant. Regarding the publications dealing with the distribution and the migration of Albacore, we found that the differentiation among the oceanic regions is consistent with the general studies but not within. Some initial studies (ex. Graves and Dizon 1989 ; Viñas et al. 1999 ; Pujolar et al. 2003) did not find significant differences between the management units probably due to the small sample size used and the lack of resolution in the markers. In current studies the genetic differences are detected using other types of markers such as the nuclear genetic. There are at least six genetically distinct stocks of albacore, located in the North and South Pacific Ocean, North and South Atlantic Ocean, the Indian Ocean and the Mediterranean Sea (Arrizabalaga et al. 2007; Chow and Ushiyama 1995; Davies et al. 2011; Takagi et al. 2001; Viñas et al. 2004; Wu et al. 2009). The gene flow between these distinct stocks of albacore seems restricted and suggests continuing to treat them as distinct management units. Doubt subsists about the heterogeneity of stocks between South Atlantic and Indian Ocean. Small numbers of albacore may undertake inter-oceanic migrations between the South Atlantic Ocean and the Indian Ocean (Beardsley 1969) and a genetic homogeneity between South Atlantic and Indian Oceans was observed (Montes et al. 2012). The distribution is nearly continuous from Angola, which captures immature albacore, to the Indian Ocean all along the edge of South Africa (Talbot and Penrith 1968). Koto (1969), Hayasi et al. (1970), Morita (1977), and Penney et al. 1992 suggested migration of albacore between the Atlantic and Indian Ocean off South Africa, which could be promoted by the strong Agulhas Current. A more exhaustive study of these regions is carried out by a new research project (GERMON by Nikolic and Bourjea), enlarging sample sizes and including samples from the western region of the Indian Ocean and the Southeastern Atlantic.

Nevertheless, the definition of six distinct stocks of albacore divisions appears more complex than usually thought. Heterogeneity seems present within all the management units, which causes a differentiation in what we could call the sub-stocks. The genetic studies, which did not detect differentiation within management units, generally did not have enough resolution in the markers (type, polymorphism and number). Microsatellites are efficient markers to detect intrapopulation heterogeneity with a minimum advocated of 30 to 40 (Barker et al. 1993; SanCristobal et al. 2006; Nikolic et al. 2009). Single nucleotide polymorphisms (SNPs) are also a relevant markers even if they show less power than do multi-allelic microsatellite loci (Ryman et al. 2006; Haas and Payseur 2011), and it takes at least 5 times more SNPs than microsatellite (Glaubitz et al. 2003) to detect fine-scale heterogeneity. Combining physically linked SNPs into haplotype blocks can increase statistical power (Gattepaille and Jakobsson 2012) but it has been estimated that up to 100 SNPs are required for accurate parentage determination in natural populations (Anderson and Garza 2006). This may explain the lack of detection of heterogeneity within oceans by Albaina et al. (2013) using 53 SNPs and it would be very interesting to increase this number.

The Mediterranean albacore populations are different compared to oceanic albacore. These populations seem to have the smallest gene flow to or from other populations, suggesting an isolation event leading to their differentiation by genetic drift (Montes et al. 2012). Heterogeneity was observed with genetic markers within the Mediterranean Sea with two populations (Davies et al. 2011). More precisely the Tyrrhenian and Adriatic Sea were grouped together and differentiated from the Balearic Sea (Montes et al. 2012). It is concordant with the different spawning areas observed in the Strait of Messina (Sanzo 1910, 1925, 1933; Sella 1924) and the Aeolian Islands (Arena 1978), then in the Balearic Islands (Serna *et al.* 2003; Garcia *et al.* 2006). The Mediterranean albacore displays separate spawning grounds (Piccinetti and Piccinetti-Manfrin 1993; Piccinetti et al. 1997) and the management in one unique stock in Mediterranean (ICCAT 1996) should be revised in two units Central-East versus West.

Concerning the potential biological heterogeneity in the North Atlantic albacore stock, proposed by Aloncle and Delaporte (1974) and Bard (1981), then discussed by Fonteneau in 2010, it seems consistent. The current study of Davies et al. (2011) indicated the potential presence of three populations across the Northeast Atlantic. This stock structure within the management unit could play a major role in the fishery trend (Fonteneau 2010) and scientific investigations are recommended. Furthermore, the potential spawning zone in the North Atlantic seems very large from the west coast to central ocean (Bard 1982; Fonteneau 2010) and extending in two seasons (Fonteneau 2010), during the second quarter in the west and the third quarter more in the central. It looks like the South Atlantic pattern with two spawning areas (west and central) (Bard 1982). Hence, we encourage analysis on



the genetic diversity on larvae in these areas covering seasons and also in the surface (upper 100 m) and deeper (around 200 m) to access the two classes (immature and mature). The presence of heterogeneity in the large spawning zone in the North Atlantic may help to understand the heterogeneity across the Northeast Atlantic. The South Atlantic needs also more investigation and genetic analysis on larvae in the two spawning areas (one in the west side and one in the central (Bard 1982)), which can be completed by sampling of immature and mature albacore to provide information on the potential presence of sub-stocks. Other studies using the habitat heterogeneity could also be encouraged. For example, to divide appropriately the entire habitat of South Atlantic albacore into sub-areas, following the results of Wu and Yeh (2002) and of a current study (Chang and Yeh 2012) providing corrections in three sub-areas.

The separation of stock is usually based on observed migration and tagging data and, more recently by genetic data. In the Pacific, the migration is not a well-defined phenomenon and it is very complex. Otsu and Uchida (1962) suggested that the migration route largely depended on age, observing that the migration area of albacore moved westward in the Pacific Ocean with age. The annual migration route for mature albacore is described as a closed ellipse wider in El Niño years than non-El Niño years and is associated with an appearance of a cold-water region in the central and south-western North Pacific (Kimura et al. 1997). Immature albacore also have an anticlockwise migration route in winter when the Kuroshio Current has a relatively straight path (Kimura et al. 1997). However, the migration does not persist when the Kuroshio takes a large meander path (Kimura et al. 1997). In spite of this complexity, there was a growing body of evidence (Laur and Lynn 1977; Laur 1983; Laur and Nishimoto (1979); Laur and Wetherall 1981; Lewis 1990) that North Pacific albacore are not as homogeneous as assumed (US. HO 1948; Clemens 1961; Otsu and Uchida 1963). The shoreward-migrating albacore of the Pacific Northwest and California seem to be independent groups (Laur and Lynn 1977) with different migratory patterns (Laur and Nishimoto 1979; Kimura et al. 1997).

Regarding the South Pacific, less is known about the movements of albacore (IATTC 2012). Using microsatellite markers, significant differences between the Southwest and Southeast Pacific albacore has been observed (Takagi et al. 2001; Montes et al. 2012). However, it is difficult to explain these genetic differentiations because no major spawning ground of albacore has been determined in the Southeast Pacific (Takagi et al. 2001). Only the two major spawning groups that have been identified in the western to mid tropical Pacific are spatiotemporally separated the North and South stocks (Nishikawa et al. 1985). Hypothesis of a sub-structuration inside each of these large spawning groups is not excluded and need more scientific investigations. Individuals from the east side of the South Pacific could come from the central spawning area. Genetic and tagging analysis of larger samples from different years classes and sizes are necessary to better define the observed genetic differences. Stock assessments are usually modeled as a single region, which simplifies the comparison since tagging data can be particularly informative about movement rates among regions (Hoyle and Langley 2007). Stock assessments of South Pacific stratified this area (in three, then four, and finally six spatial strata) in order to account for the distinctive size segregation by latitude (Hoyle et al. 2012). Heterogeneity present in all management units causes a number of problems with the assessment because it is essential that the stock assumed corresponds to the real population structure of the resource.

## **V. Conclusion**

Given that most stocks of albacore are currently overexploited, an urgent need exists to improve conservation and management efforts, including the development of alternative methods of population assessment (Collette et al. 2011; Juan-Jordá et al. 2011; Albaina et al. 2013). It is essential that the stock assumed during the assessment and management process corresponds to the real population structure of the resource (Arrizabalaga et al. 2007). 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)). Genetic methods may aid a previous investigation to identify population structure (Hoarau et al. 2004; Carlsson et al. 2006; Was et al. 2008; Kovach et al. 2010). Genetic studies should be continued by increasing the sample size and number of markers to achieve a clear distinction between and within the stocks. The Northeast Atlantic and Mediterranean Sea seems clearly divided in several stocks. Conventional tagging and electronic tags would also assist to investigate the stock structure and seasonal migrations and habitat distribution. The South Atlantic and Pacific differences observed between the west and east really need to be investigated. The Indian Ocean is the oceanic region in which we have the least knowledge but the last management committee has encouraged studies on the population structure (IOTC-SC15 2012) and some are already in process.

## Acknowledgements

Gilles Morandau and Nathalie Cail Milly from IFREMER (Anglet) are deeply acknowledged for their comments facilitating this working paper.

## References

Albaina A, Iriondo M, Velado I, Laconcha U, Zarraindia 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*.

Allendorf FW, Ryman N, Utter FM. 1987. Genetics and fishery management: past, present and future. In *Population genetics and fishery management* (N. Ryman and F. M. Utter, eds.), p. 1–19. Univ. Washington Press, Seattle and London.

Aloncle H, Delaporte F. 1979. Nouvelles remarques sur la structure du stock de germons (*T. alalunga*) dans le nord-est Atlantique. *ICCAT. Col. Vol. Sci. Pap.* 8(2): 261-264.

Aloncle H, Delaporte F. 1976. Marquages de germons par l'ISTPM, 1967-1974. *ICCAT. Col. Vol. Sci. Pap.* 5: 216-220.

Aloncle H, Delaporte F. 1974. 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.

Aloncle H, Delaporte F, Forest A, Leroy C. 1976. Campagnes thonières 1975 de l'ISTPM. Nouvelles données sur la pêche et connaissance du germon. *Science et Pêche, Bull. Inst. Pêches marit.* 256: 15pp.

Anderson EC, Garza JC. 2006. The power of single-nucleotide polymorphisms for large-scale parentage inference. *Genetics* 172:2567-2582.

Arena P. 1978. Aspects biologiques et comportements des concentrations génétiques du thon rouge en Méditerranée. *Actes Coll. CNEXO* 8: 53-57.

Arrizabalaga H, Lopez-Rodas V, Costas E, González-Garcás A. 2007. 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. *Fisheries Bulletin* 105, 140–6.

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.

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, Lopez-Rodas V, Ortiz 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 Release- Recapture Experiences. *ICCAT Col Vol Sci Pap* 54:1479–1494.

Bard FX. 1982. L'habitat du germon (*Thunnus alalunga*) en Océan Atlantique. *Collect. Vol. Sci. Pap. ICCAT*, 17(2): 487-490.

Bard FX. 1981. La thon germon (*Thunnus alalunga*) de l'Océan Atlantique. De la dynamique de population à la stratégie démographique. Thèse Doctorat ès Sciences Naturelles, Université de Paris VI, 330P.

Barker JSF, Bradley DG, Fries R, Hill WG, Nei M, Wayne RK. 1993. An integrated global programme to establish the genetic relationships among the breeds of each domestic animal species. Rome: FAO Animal Production and Health Paper, Report of a working group.

- Beardsley GL. 1969. Proposed Migrations of Albacore, *Thunnus alalunga*, in the Atlantic Ocean. Transactions of the American Fisheries Society 98. 4: 589-598.
- Begg GA, Friedland KD, Pearce JB. 1999. Stock identification and its role in stock assessment and fisheries management: an overview. Fisheries Research 43:1-8.
- Begg GA, Waldman JR. 1999. An holistic approach to fish stock identification. Fisheries Research, 43:35-44.
- 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 Journal of Marine Science.
- Chand FC, Yeh SY. 2012. Standardized CPUE of the South Atlantic albacore (*Thunnus alalunga*) based on Taiwanese longline catch and effort statistics dating from 1967 and 2010. Collect. Vol. Sci. Pap. ICCAT, 68(2): 580-592.
- 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.
- Chow S, Kishino H. 1995. Phylogenetic relationships between tuna species of the genus *Thunnus* (Scombridae: Teleostei): inconsistent implications from morphology, nuclear and mitochondrial genomes. Journal of Molecular Evolution 41, 741-8.
- Clemens HB. 1961. The migration, age, and growth of Pacific albacore (*Thunnus germon*), 1951-1958. Calif. Dept. Fish and Game, Fisheries Bulletin. 115, 128 p.
- Collette BB, Carpenter K.E, Polidoro B.A. et al. 2011. High value and long life-double jeopardy for tunas and billfishes. Science, 333, 291-2.
- Davies CA, Gosling EM, Was A, Brophy D, Tysklind N. 2011. Microsatellite analysis of albacore tuna (*Thunnus alalunga*): population genetic structure in the North-East Atlantic Ocean and Mediterranean Sea. Marine Biology 158: 2727-2740.
- De Metrio G, Megalofonou P, Cacucci M, Sion L, Ortiz de Zarate V, Acone, F. 1997. Results of tagging experiments on albacore (*Thunnus alalunga* Bonn.) in the Northern Ionian and Southern Adriatic Seas from 1990 to 1995. ICCAT Collective Volume of Scientific Papers 46, 148-151.
- Dicenta A, Piccinetti C. 1978. Desove de atún (*Thunnus thynnus* L.) en el Mediterráneo occidental y evaluación directa del stock de reproductores, basado en la abundancia de sus larvas. ICCAT. Col. Vol. Sci. Pap. 7(2): 389-395.
- Farley JH, Williams AJ, Hoyle SD, Davies CR, Nicol SJ. 2013. Reproductive dynamics and potential annual fecundity of the South Pacific Albacore tuna (*Thunnus alalunga*). Plos One 8(4).
- Fonteneau A. 2010. On the North Atlantic Albacore stock and on its potential sub populations. Collect. Vol. Sci. Pap. ICCAT, 65(4): 1282-1290 (2010).
- Garcia A, Cortes D, Ramirez T, Fehri-Bedoui R, Alemany F, et al. 2006. First data on growth and nucleic acid and protein content of field-captured Mediterranean bluefin (*Thunnus thynnus*) and albacore (*Thunnus alalunga*) tuna larvae: a comparative study Scientia Marina (Barcelona), suppl. Suppl. 2 70 : 67-78.
- Gattepaille LM, Jokobsson M. 2012 Combining markers into haplotypes can improve population structure inference. Genetics 190, 159-74.
- Glaubitz JC. et al . 2003. Prospects for inferring pairwise relationships with single nucleotide polymorphisms. Molecular Ecology.12, 1039-1047.
- Godsil HC. 1948. A preliminary population study of the yellowfin and the albacore. The California Department of Fish and Game's Fish Bulletin. 70:1-90

- Goni N, Logan J, Arrizabalaga H, Jarry M, Lutcavage M. 2011. Variability of albacore (*Thunnus alalunga*) diet in the Northeast Atlantic and Mediterranean Sea. *Marine Biology* 10 : 1057-1073.
- Graves JE, Dizon AE. 1989. Mitochondrial DNA sequence similarity of Atlantic and Pacific albacore tuna (*Thunnus alalunga*). *Canadian Journal of Fisheries and Aquatic Sciences*. 46: 870-873.
- Haasl RJ, Payseur BA. 2011. Multi-locus inference of population structure: a comparison between single nucleotide polymorphisms and microsatellites. *Heredity* 106, 158–71.
- Hallaire L, Dao JC. 1971. Etude sérologique du germon du nord-est Atlantique. Cons. Perm. Inst. Cons. Thon. Atlant. Madrid 1971.
- 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 Fish.Res.Lab.S, Series No. 3*, pp. 18–72
- 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. *Journal of Sea Research*.
- Hoyle S, Hampton J, Davies N. 2012. Stock assessment of albacore tuna in the south Pacific Ocean. SPC, Busan, Republic of Korea. Scientific Committee Eighth Regular Session. WCPFC-SC8-2012/SA-WP-04-REV1.
- Hoyle S, Langley A. 2007. Comparison of South Pacific Albacore stock assessments using MULTIFAN-CL and Stock Synthesis 2. Scientific Committee Third Regular Session. Honolulu, United States of America. WCPFC-SC3-ME SWG/WP-6
- Hue SB. 1979. Recherches sur l'hétérogénéité du stock de germon *T. alalunga* du NE Atlantique par électrophorese. ICCAT. Col. Vol. Sci. Pap. 8(2): 265-271.
- Hue SB. 1980a. New knowledge on the migration of albacore (*T. alalunga*) in the Northeast Atlantic. ICCAT. Col. Vol. Sci. Pap. 9(2): 344-352.
- Hue SB. 1980b. Summary of the study on the heterogeneity of the stock of albacore (*T. alalunga*) in the Northeast Atlantic. ICCAT. Col. Vol. Sci. Pap. 9(2): 353-355.
- 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.
- IATTC. 2012. Fishery Status Report N°10. Tunas and Billfishes in the Eastern Pacific Ocean in 2011. La Jolla, California 2012.
- ICCAT. 2011. Report of the 2010 ICCAT Mediterranean Albacore data preparatory meeting. ICCAT, 66(5): 1809-1856. Available : [http://www.iccat.int/Documents/CVSP/CV066\\_2011/no\\_5/CV066051809.pdf](http://www.iccat.int/Documents/CVSP/CV066_2011/no_5/CV066051809.pdf)
- ICCAT. 1996. Report of the final meeting of the ICCAT Albacore Research Program. Sukarrieta, Vizcaya.
- IOTC–SC15. 2012. Report of the Fifteenth Session of the IOTC Scientific Committee. Mahé, Seychelles, 10–15 December 2012. IOTC–2012–SC15–R[E].
- Ishii T. 1965. Morphometric analysis of the Atlantic albacore populations mainly her eastern areas. *Bulletin of the Japanese Society of Scientific Fisheries* 31: 333-339 (in Japanese with English abstract).
- Juan-Jordá MJ, Mosqueira I, Cooper A.B, Freire J, Dulvy NK. 2011. Global population trajectories of tunas and their relatives. *Proceedings of the National Academy of Sciences of the United States of America* 108, 20650–5.
- Keyvanfar A. 1962. Sérologie et immunologie de deux espèces de thonidés (*Germo Alalunga* GMELIN et *Thunnus Thynnus* LINNÉ) de l'Atlantique et de la Méditerranée. *Revue des Travaux de l'Institut des Pêches Maritimes*. 26 (4).

- Kimura S, Nakai M, Sugimoto T. 1997. Migration of albacore, *Thunnus alalunga*, in the North Pacific Ocean in relation to large oceanic phenomena . Fisheries Oceanography. 6:51–57.
- 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).
- 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. Marine Ecology Progress Series.
- Kurogane K, Hiyama Y. 1958. Morphometric comparison of the albacore from the northwest, the equatorial and the southwest Pacific. Records of oceanographic Works in Japan 4:67-75.
- Kurogane K, Hiyama Y. 1959. Morphometric comparison of the albacore from the Indian and the Pacific Ocean. Records of oceanographic Works in Japan 5:68-84.
- Laurs RM. 1983. The North Pacific albacore - an important visitor to California Current water. Calif. Coop. Oceanic Fish. Invest. Rep. 24:99-106.
- Laurs RM, Wetherall JA. 1981. Growth rates of North Pacific albacore, *Thunnus alalunga*, based on tag returns. Fishery Bulletin 79 (2): 293-302.
- Laurs RM, Lynn RJ. 1977. Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: distribution relative abundance, and association with Transition Zone waters. Fishery Bulletin. U.S. 75:795-822.
- Laurs RM, Nishimoto RN. 1979. Results from North Pacific albacore tagging studies. Southwest Fisheries Center Admin. Rept. No. LJ-79-17, 9 p.
- Lewis AD. 1990. South Pacific albacore stock structure: a review of available information. 3rd South Pacific Commission, Noumea, New Caledonia, p. 1–13.
- Mele S, Merella P, Macias D, Gomez MJ, Garippa G, et al. 2010. Metazoan gill parasites of wild albacore *Thunnus alalunga* (Bonaterre, 1788) from the Balearic Sea (western Mediterranean) and their use as biological tags. Fisheries Research (Amsterdam) 102. 3 : 305-310.
- Metcalf D. 2006 Fish population structuring in the North Sea: understanding processes and mechanisms from studies of the movements of adults. Journal of Fish Biology, 69 (supplement C): 48-65.
- 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.
- 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. Journal of Fish Biology 66, 1545–57.
- Nakamura H. 1969. Tuna distribution and migration. Fishing News Ltd, London.
- Nishikawa Y, Honma M, Ueyanagi S, Kikawa S. 1985. Average distribution of larvae of oceanic species of scombroid fishes, 1956-1981. Far Seas Fish Res Lab S Ser 12: 1–99.
- Nikolic N, Fève K, Chevalet C, Høyheim B, Riquet J. 2009. A set of 37 microsatellite DNA markers for genetic diversity and structure analysis of Atlantic salmon *Salmo salar* populations. Journal of Fish Biology 74, 458–466.

- Ortiz de Zárate V, Cort JL. 1998. Albacore (*Thunnus alalunga*, Bonaterre) stock structure in the Atlantic ocean as inferred from distribution and migration patterns. ICCAT TUNA SYMPOSIUM, ICCAT, Col. Sci. Pap. Vol. L (1) pp: 251-260.
- Otsu T, Uchida RN. 1963. Model of the migration of albacore in the North Pacific Ocean. U.S. Fish and Wildlife Service. Fishery Bulletin. 63: 33-44.
- 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, 37: 218-229.
- Piccinetti C, Piccinetti-Manfrin G. 1993. Distribution des larves de thonidés en Méditerranée. ICCAT Collective Volume of Scientific Papers 40, 164–172.
- Piccinetti C, Piccinetti-Manfrin G, Soro S. 1997. Results of a research survey on tuna larvae in the Mediterranean. ICCAT Collective Volume of Scientific Papers 46, 207–214.
- Pujolar JM, Roldán MI, Pla C. 2003. Genetic analysis of tuna populations, *Thunnus thynnus thynnus* and *T. alalunga*. Marine Biology 143: 613–621
- Riccioni G, Landi M, Ferrara G, Milano I, Cariani A, Zane L, Sella M, Barbujani G, Tinti F. 2010. Spatio-temporal population structuring and genetic diversity retention in depleted Atlantic bluefin tuna of the Mediterranean Sea. Proceedings of the National Academy of Sciences of the United States of America 107, 2102–7.
- Ryman N, Palm S, André C, Carvalho G.R, Dahlgren T.G, Jorde P.E, Laikre L, Larsson L.C, Palmá A, Ruzzante D.E. 2006. Power for detecting genetic divergence: differences between statistical methods and marker loci. Molecular Ecology 15, 2031–45.
- SanCristobal M, Chevalet C, Haley CS, Joosten R, Rattink AP, Harlizius B, Groenen MAM, Amigues Y, Boscher M-Y, Russell G, Law A, Davoli R, Russo V, Désautés C, Alderson L, Fimland E, Bagga M, Delgado JV, Vegapla JL, Martinez AM, Ramos M, Glodek P, Meyer JN, Gandini GC, Matassino D, Plastow GS, Siggens K, Laval G, Archibald AL, Milan D, Hammond K, Cardellino R. 2006. Genetic diversity within and between European pig breeds using microsatellite markers. Animal Genetics 37, 189–198.
- Sanzo L. 1910. Uova e larve di Scomberoidei (Riv. Pesce. e Idrobiol). N°9.
- Sanzo L. 1925. Uova e larve di Alalonga. *Orcynus germo* Ltk. An. R. Ace. Dei Linei (6) pp. 131-134.
- Sanzo L. 1933. Uova e primi stadi larvali di Alalonga. (*Orcynus germo* Ltkn). H. Comit Talassog. Ital. Mem. CXC VIII, p. 10.
- Sella M. 1924. Caratteri differenziali dei giovani stadi di *Orcynus thynnus* Ltkn, O. Alalonga Risso, *Auxis bisus* sp. Bencic Real Acead. Dei Linei 5me Série XXXIII, p. 300-305.
- Serene P. 1971. Esterase of the northeast Atlantic albacore stock. CIEM CM. 1969 Special Meeting on "The Biochemical and Serological Identification of fish stocks", 33 : 1-6.
- Serna JM, Valeiras J, Alot E, Godoy D. 2003. Collective volume of scientific papers. International Commission for the Conservation of Atlantic Tunas/Recueil de documents scientifiques. Commission internationale pour la Conservation des Thonides de l'Atlantique/Coleccion de documentos científicos. Comision internacional para la Conservacion del Atun Atlantico 55. 1: 160-165.
- Shiohama T. 1971. Studies on measuring changes in the character of the fishing effort of the tuna longline fishery. Concentrations of the fishing effort to particular areas and species in the Japanese fishery. Bull. Far Seas Fish. Lab. 5: 107-130.
- Shiohama T. 1973. Overall fishing intensity and catch by length class of albacore in Japanese Atlantic longline fishery, 1956-1970. ICCAT Recueil de documents scientifiques, vol. 1: 198-224.

- Shiohama T. 1974. Overall fishing intensity and catch by length class of albacore in Japanese Atlantic longline, 1956-1971. ICCAT Recueil de documents scientifiques, vol. 11: 163-176.
- Suda A. 1974. Recent status of resources of tuna exploited by longline fishery in the Indian Ocean. Bull. Far Seas Fish. Res. Lab. 10:27-62.
- Suzuki A. 1962. Serological studies of the races of tuna. VI. Bigeye-3 antigen occurred in the albacore. Rep Nankai Reg Fish Res Lab 16:67-70 (in Japanese with English abstract)
- Takagi M, Okamura T, Chow S, Taniguchi N. 2001. Preliminary study of albacore (*Thunnus alalunga*) stock differentiation inferred from microsatellite DNA analysis. Fishery Bulletin, 99: 697-701.
- Talbot FH, Penrith MJ. 1963. Synopsis of biological data on species of the genus *Thunnus sensu lato* (South Africa). FAO Fish. Rep., (6) Vol. 4 : 608-46.
- 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*. Bull. Far Seas Fish. Res. Lab. 2:177-219.
- Uozumi Y. 1996. A historical review of Japanese longline fishery and albacore catch in the Atlantic Ocean. ICCAT Coll. Vol. Sci. Pap.; XLIII; 261-268.
- U. S. Hydrographic office 1948. World atlas of sea surface temperatures. 2nd ed., 1944. Wash., Gov't Print. off., H. O. no. 225.
- Viñas J, Alvarado Bremer JR, Pla C. 2004. Inter-oceanic genetic differentiation among albacore (*Thunnus alalunga*) populations. Marine Biology 145: 225-232.
- Viñas J, Santiago J, Pla C. 1999. Genetic characterisation and Atlantic Mediterranean stock structure of albacore, *Thunnus alalunga*. Collect Vol Sci Pap ICCAT 49: 188-190.
- Viñas J, Santiago J, Pla C. 1999. Genetic characterization and Atlantic Mediterranean stock structure of Albacore, *Thunnus alalunga*. ICCAT Coll Vol Sci Pap 49:188-191.
- Was A, Gosling E, McCrann K, Mork J. 2008. Evidence for population structuring of blue whiting (*Micromesistius poutassou*) in the Northeast Atlantic. ICES Journal of Marine Science.
- Williams AJ, Farley JH, Hoyle SD, Davies CR, Nicol SJ (2012) Spatial and sex-specific variation in growth of albacore tuna (*Thunnus alalunga*) across the South Pacific Ocean. PloS One 7(6): 1-10.
- 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. Fisheries Research 95: 125-131.
- Wu CL, Yeh SY. 2002. Geographic distribution and area demarcation on the fisheries resource of south Atlantic albacore. ACTA Oceanogra. Taiwan. 40(1):81-92.
- 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
- 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 GP, Xu LX, Zhou YQ, Dai XJ. 2008. Length-frequency compositions and weight-length relations for bigeye tuna, yellowfin tuna, and albacore (Perciformes: Scombrinae) in the Atlantic, Indian, and Eastern Pacific Oceans. Acta Ichthyol. Piscatoria, 38(2): 157-161.