

DIFFERENTIATION OF ALBACORE STOCK: REVIEW BY OCEANIC REGIONS

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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.

RESUMEN

Dado que uno de los problemas más comunes en las pesquerías es la definición de unidades de ordenación en este documento se propone una revisión bibliométrica centrada en la diferenciación de las poblaciones de atún blanco (Thunnus alalunga) entre y dentro de las regiones oceánicas (océanos Atlántico, Pacífico e Índico y mar Mediterráneo). Este documento es el primer paso de una revisión global del atún blanco realizada mediante el uso de la base de datos acuática internacional (ASFA). En el documento se analizaron 367 publicaciones, sobre todo compuestas de artículos científicos (64%), pero también incluía la revisión de documentos, actas e informes de conferencias (24%) y libros (12%). Se puede observar que debido a las divergencias en los resultados, el concepto de stock y su delimitación sigue siendo un tema controvertido. Dichas conclusiones nos llevan a creer en la urgente necesidad de realizar estudios adicionales centrados en esta especie actualmente sobreexplotada en la mayoría de las regiones del mundo, con el fin de mejorar las unidades de ordenación utilizadas actualmente por las organizaciones regionales para fines de ordenación de pesquerías.

KEYWORDS

Albacore, stock, structure, distribution, Thunnus alalunga

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1. 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).

2. 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.

3. 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 shown by the greater part of publications and is in agreement with the management units taken 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.

4. 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; San Cristobal *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 Jokobsson 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 (Lauris and Lynn 1977; Lauris 1983; Lauris and Nishimoto (1979); Lauris 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 (Lauris and Lynn 1977) with different migratory patterns (Lauris 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-structuring 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.

I. 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.

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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 Metrio <i>et al.</i> 1997	Tagging	Low migration between Mediterranean and Atlantic	x	
	x		Ortiz and Cort 1998	Tagging	Low migration between Mediterranean and Atlantic	x	
		x	Viñas <i>et al.</i> 1999	Genetic	No differences between albacores from the Mediterranean Sea and those from the Atlantic		x
		x	Pujolar <i>et al.</i> 2003	Genetic	No genetic heterogeneity was observed between Mediterranean and Azores (East Atlantic) samples		x
	x		Arrizabalaga <i>et al.</i> 2002, 2003	Tagging	Low migration between Mediterranean and Atlantic	x	
	x		Arrizabalaga <i>et al.</i> 2004	Lectins in blood groups	Mediterranean and North Atlantic populations are distant	x	
	x		Viñas <i>et al.</i> 2004	Genetic	Differentiation between NE Atlantic and Mediterranean	x	
	x		Nakadate <i>et al.</i> 2005	Genetic	Strong frequency differences between Atlantic and Mediterranean samples. Low gene flow between Mediterranean and Atlantic	x	
	x		Goni <i>et al.</i> 2011	Diet, Isotope	High difference between Mediterranean and Northeast Atlantic	x	
	x		Mele <i>et al.</i> 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 <i>et al.</i> 2011	Genetic	NE Atlantic and Mediterranean are strongly differentiated	x	
	x		Montes <i>et al.</i> 2012	Genetic	Distinguished the Mediterranean Sea population from the rest	x	
		Albaina <i>et al.</i> 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 <i>et al.</i> 1995	Morphometric, Genetic	Possible 2 stocks: south Atlantic and Indian	x	
	x		Yeh <i>et al.</i> 1997	Genetic	South Atlantic differs of East Indian	x	
	x		Zhu <i>et al.</i> 2008	Length	Differences North Atlantic and West Indian	x	
		x	Montes <i>et al.</i> 2012	Genetic	Homogeneity between South Atlantic and Indian Oceans		x
	x		Albaina <i>et al.</i> 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	

Atlantic - Pacific	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 <i>et al.</i> 2001	Genetic	Differentiation within and between the Pacific and Atlantic	x	
	x		Zhu <i>et al.</i> 2008	Length	Differences North Atlantic and Southeast Pacific	x	
	x		Davies <i>et al.</i> 2011	Genetic	NE Atlantic and SW Pacific are strongly differentiated	x	
	x		Albaina <i>et al.</i> 2013	Genetic	Significant heterogeneity between oceans	x	
Pacific - 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		Lewis 1990	review: Catch, Morphometric, Tagging	Limited interchange	x	
	x		Chow and Kishino 1995	Genetic	Differentiation between Indo-Pacific albacore	x	
	x		Zhu <i>et al.</i> 2008	Length	Differences West Indian and Southeast Pacific	x	
	x		Montes <i>et al.</i> 2012	Genetic	Differentiation between Pacific and Indian albacore	x	
	x		Albaina <i>et al.</i> 2013	Genetic	Significant heterogeneity between oceans but Indian Ocean albacore were differentiated to a small degree from Pacific Ocean albacore	x	
Pacific - Mediterranean	x		Davies <i>et al.</i> 2011	Genetic	Mediterranean and SW Pacific are strongly differentiated	x	
	x		Montes <i>et al.</i> 2012	Genetic	Distinguished the Mediterranean Sea population from the rest	x	
Indian - Mediterranean	x		Montes <i>et al.</i> 2012	Genetic	Distinguished the Mediterranean Sea population from the rest	x	
	x		Albaina <i>et al.</i> 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	

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 <i>et al.</i> 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 <i>et al.</i> 2001	Genetic	Differences between the 2 Atlantic hemisphere samples (NEA and SWA)	x		
		x		Arrizabalaga <i>et al.</i> 2002	Tagging	No albacore released in the North Atlantic or the Mediterranean has been recaptured in the South Atlantic.	x		
			x	Nakadate <i>et al.</i> 2005	Genetic	Differences significant between the samples from the Atlantic (NEA and SWA)		x	
			x	Montes <i>et al.</i> 2012	Genetic	However the samples of Bay of Biscay was nearest of the South Atlantic than the North (Ireland) samples.		x	
		x	Albaina <i>et al.</i> 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 <i>et al.</i> 2001	Genetic	NE Atlantic sample was significantly heterogeneous		x
		x		Davies <i>et al.</i> 2011	Genetic	3 populations across the NEA		x
		x		Chand and Yeh 2012	Catch	South Atlantic in 3 sub-areas		
			x	Albaina <i>et al.</i> 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 <i>et al.</i> 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 <i>et al.</i> 2003	Genetic	No genetic heterogeneity was observed within Mediterranean samples	x	
			x	Nakadate <i>et al.</i> 2005	Genetic	No significant heterogeneity between central and east	x	
		x		Goni <i>et al.</i> 2011	Diet, Isotope	Consistent with the existence of separate spawning grounds in the Tyrrhenian Sea and in the South Adriatic Sea		x
		x		Davies <i>et al.</i> 2011	Genetic	2 populations East and West		x
		x		Montes <i>et al.</i> 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 <i>et al.</i> 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 Ushiana 1995	Genetic	No heterogeneity between North and South		x
		x		Takagi <i>et al.</i> 2001	Genetic	Differences between the 2 Pacific hemisphere samples. Each one has a large spawning group from west to mid tropical	x	
			x	Montes <i>et al.</i> 2012	Genetic	No differences between North and South Pacific		x
		x		Aranda <i>et al.</i> 2010	Tagging	Separation north and south	x	
				x	Albaina <i>et al.</i> 2013	Genetic	No differences between northern and southern populations	
	Within	x		Godsil 1948	Morphometric	Morphometric differences between western and eastern Pacific		x

	management units		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		Laurs and Lynn 1977	Tagging, Length	Evidence that the shoreward-migrating albacore of the Pacific Northwest and California are independent groups		x
		x		Laurs and Nishimoto 1979	Tagging	Two substocks constitute the North with different migratory patterns		x
		x		Laurs and Wetherall 1981	Tagging, morphometric	Different growth rates and length frequency in two groups of North Pacific		x
		x		Laurs 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 <i>et al.</i> 2001	Genetic	Differences between Southwest and Southeast Pacific		x
		x		Montes <i>et al.</i> 2012	Genetic	2 populations in the south: East and West		x
		x		Williams <i>et al.</i> 2012	Length	Variation in length-at age and growth parameters across longitudes in South Atlantic from west to central		x
		x		Farley <i>et al.</i> 2013	Morphometric	Albacore in easterly longitudes on average having heavier gonads for their size than fish further west (South Pacific)		x
			x	Albaina <i>et al.</i> 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
		x		Hsu 1994	Catch, Morphometric	Size composition varies with latitude		x
		x		Yeh <i>et al.</i> 1995	Genetic, Morphometric	Possible two stocks delimited by the 90°E longitude		x
		x		Yeh <i>et al.</i> 1997	Genetic	The variation between group is higher than within group		x
		x		Nishikawa <i>et al.</i> 1985	Catch larvae	Two spawning areas, in the east (near madagascar) and the west side		x
			x	Albaina <i>et al.</i> 2013	Genetic	No within-ocean heterogeneity	x	