Population structure and management of Albacore tuna (*Thunnus alalunga)* in the North Atlantic Ocean

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Declaration of PhD Thesis

I hereby declare that the work contained in this thesis is my own except where explicitly stated otherwise in the text and that it has not been submitted, in whole or in part for another degree.

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Abstract

Population structure and management of Albacore tuna

(*Thunnus alalunga)* in the North Atlantic Ocean

Roxanne Duncan

Albacore tuna *(Thunnus alalunga)* is a globally important species found in the tropical and temperate zones of every ocean including the Mediterranean Sea. The aim of this research is to advance the current knowledge concerning the population structure of albacore tuna in the North Atlantic Ocean as well as to improve fishery-dependent estimates of its relative abundance using vessel monitoring data from the Irish mid-water pair trawl fleet. The population structure was investigated at both a local and regional scale. At the local scale, otoliths from juveniles caught within the Bay of Biscay and off its western shelf were examined in order to determine their stock structure using otolith shape analysis. Results from the study revealed significant differences in otolith shape between the two areas. At the regional scale, otolith microchemistry and microstructure analyses were conducted on otoliths from juveniles, caught in and around the Bay of Biscay, and from adults collected in the offshore fisheries of Canada and Venezuela to determine if they shared similar larval or pre-juvenile habitats. The study revealed, based on the microchemistry analysis of the larval core, that there may be more than one spawning location in the North Atlantic for albacore tuna. The final study investigated the use of fishery-dependent data to derive indices of abundance. Vessel monitoring systems (VMS) data from the Irish pair trawl fishery were used to identify fishing pairs targeting albacore tuna from 2006-2016. A hidden semi-Markov model was used to infer fishing effort from VMS data. The impact of using fishing effort instead of days at sea was also compared using CPUE standardisation models. The results showed that hidden semi-Markov models are efficient at inferring fishing effort and that using VMS data to describe fleet behaviour can improve catch rate standardisation for albacore tuna.

Chapter 1: Introduction

1.1 Definition of a Stock

A stock can be simply defined as a discrete group of fish whose internal dynamics are monitored in order to detect changes in response to an external force such as fishing (Secor, 2013). There are numerous ways to define a stock, with each definition depending on the primary reason for the maintenance of the group. Biologically, a stock is a population of fish that is large enough to be self-reproducing, and whose members exhibit similar life history characteristics, that may not be genetically distinct from another population (Hilborn and Walters, 1992). A population is defined as a group of individuals of the same species that is genetically and spatially separated from other groups (Fonteneau, 2010; Wells and Richmond, 1995). From a management standpoint, a stock is a unit of management created to ensure the sustainable utilisation of a resource, for biological, social, recreational and economic reasons (Begg and Waldman, 1999; Cochrane and Garcia, 2009). Using this definition enables species to be properly assessed and minimises fishing impacts on the environment and on non-target species (Cochrane and Garcia, 2009). To ensure that a stock is sustainably exploited and not in an overfished state, stock assessments are carried out by fisheries scientists. Stock assessments, which can be carried out on both single and multiple species, are used to determine the past and present state of the stock as well as try to predict how the stock would respond to changes in management, e.g. changes in quotas and lengths of fishing seasons (Cooper, 2006; Methot and Wetzel, 2013).

1.2 Importance of Proper Stock Management

Information from stock assessments is crucial to ensure that a stock is not overexploited or worse, reaches such low levels that it is not able to replenish itself, and eventually collapses. One infamous example of stock mismanagement is the Newfoundland cod, *Gadus morhua*, fishery. According to Atkinson et al. (1997), the cod fishery had existed since the 1500s, first targeting cod in the inshore waters then moving offshore with the introduction of otter trawling into the area in the 1950s. Annual catches quickly increased from approximately 150 000 tonnes to 810 000 tonnes by 1968. As a result of the rapid increase in catches, the stock declined and only increased in 1988 due to the extension of the Canadian Exclusive Economic zone in 1978. By 1991, fishery independent surveys and studies reported a decrease in cod both in the inshore and offshore waters. In 1992,

the moratorium to close the fishery was implemented based on the recommendation of the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) and the Northwest Atlantic Fisheries Organisation (Atkinson et al., 1997). The impact of this decision to close the fishery drastically affected the region, especially Newfoundland which had relied on the cod fishery for centuries (Gien, 2000). To this day, the fishery still remains closed.

1.3 Methods for Stock Identification

In many instances, the boundaries of a stock may not be consistent with the spatial extent of the species' population. From a biological point of view, a stock should take into consideration the population structure of the species to ensure its proper management (Carvalho and Hauser, 1994). Understanding the population structure equips scientists with information relating to the genetic framework of the species, its life cycles and internal dynamics in terms of stability and resilience to natural and anthropogenic effects (Kerr et al., 2010a; Ruzzante et al., 2006). This information will in turn help managers make more informed decisions on the management of the stock. The characteristics present within a population can be due to genetic, demographic and environmental differences (Heino, 2013; Waldman, 2005).

The investigation into the genetic differences between stocks has allowed scientists to assign individuals or subpopulations to a specific stock, to outline stock boundaries, and to estimate population size (Mariani and Bekkevold, 2013). In many highly migratory species, the genetic differentiation required to characterise the stock and to establish its boundaries is very low (Hauser and Carvalho, 2008; Palstra and Ruzzante, 2008). This could be due to small numbers of individuals moving between populations every generation. This may increase the genetic similarity between stocks, but if one stock is heavily fished or severely mismanaged, these movements will not be enough to replace it. Even though the stocks may be considered genetically similar, there may exist phenotypic differences which would enable individuals within the stock to adapt to differences in the environment e.g. temperature, salinity and oxygen content (Mariani and Bekkevold, 2013; Nielsen et al., 2009; Wright et al., 2002).

Phenotypic traits such as body size and shape, colouration, even the numbers of scales or fin rays on the fish can result from not only genetic differences but also from differences

in life history and environment (Heino, 2013). Differences in life histories are recorded in growth marks which are proportional and independent of somatic growth (Wright et al., 2002). These marks are used in age determination and stock identification studies; they are used to calculate the age and growth rate of fish, detect differences in growth histories of sub-populations and identify the stage when they separated from each other (Brophy, 2013; Campana and Thorrold, 2001; Pepin et al., 2001). Otoliths, scales and fin spines are hard structures frequently used in the analysis of growth marks which are deposited at different timescales (annual, seasonal, daily) (Brophy, 2013; Panfili et al., 2002).

Of the three structures, otoliths are the most extensively used to understand the population structure of teleost species, from marine to freshwater environments. Otoliths are widely used because it is metabolic stability and continual growth throughout the fish's life. These characteristics are not always observed in scales and fin spines, especially in older fish and fish that have experienced poor growth during their lives, therefore their use has been limited (Campana and Thorrold, 2001). Otoliths begin forming in the embryonic life stage and record the growth marks of the fish's development in a chronological manner (Campana and Thorrold, 2001). The growth marks, termed microstructure, can also be used to identify development stages, such as hatch time and metamorphosis in order to reconstruct life histories and understand population structure (Baumann et al., 2015; Morales-Nin and Geffen, 2015; Toole et al., 1993).

Fish that inhabit different environmental conditions for portions of their lives can be discerned using the microchemical composition of otoliths. Microchemistry analyses involve measuring the concentrations of stable isotope ratios and trace metals in otoliths using various techniques, for example, gas-ratio spectrometry (Fraile et al., 2016; Niklitschek et al., 2010), inductively coupled plasma mass spectroscopy of whole or sections of otoliths (Campana et al., 2000), electron probe microanalysis and micro-proton induced X-ray emission analysis (Proctor et al., 1996; Thresher, 1999). Preliminary studies in the 1960s showcased otolith microchemistry as a method that could delineate a population's structure and its migration history based on the premise that there was a direct relationship between the chemistry of the otolith and the chemistry of the environment (Thresher, 1999). However, by the late 1990s, it became apparent that otolith microchemistry was not only influenced by the seawater's chemical composition but also by environmental and physiological factors, such as diet and temperature (Sturrock et al.,

2012; Thresher, 1999). This realisation caused scientists to re-evaluate their approach to using otolith microchemistry and to investigate how these factors influenced the composition of otoliths. Otolith microchemistry has been used to reveal information about the movement patterns (Elsdon et al., 2008), metabolism (Sherwood and Rose, 2003), spawning sites (Rooker et al., 2014) and population structure (Campana et al., 2000) of a stock.

The shape of otoliths and scales has been found to be an effective tool in detecting inter- and intra-specific differences originating from genetic and environmental influences (Richards and Esteves, 1997; Schulz-Mirbach et al., 2008; Vignon and Morat, 2010). Otolith shape is species specific and is influenced by genetics, ontogeny and the environment; and in previous studies, it has been shown to be affected by differences in temperature, salinity, substrate type and water depth (Keating et al., 2014). This type of analysis utilises different techniques to describe and compare the otolith shape such as wavelet analysis, biorthogonal grids, thin plate splines, Euclidean distance matrices and variations of the Fourier series (polar and elliptical) (Cadrin and Friedland, 1999; Tracey et al., 2006). These techniques quantify boundary shapes so that variations in the otolith shape can be evaluated. The most widely used technique is Elliptical Fourier series which fits harmonics to the shape of the otolith or other hard structure (Beyer and Szedlmayer, 2010; Burke et al., 2008; Chen et al., 2000) and is capable of discerning subtle shape variations among groups (Benzinou et al., 2013; Stransky et al., 2008a).

Both otolith microchemistry and otolith shape have been essential tools for understanding population structure and identifying stock boundaries in both marine and freshwater species; however, the way otoliths are used, and the information gathered from either tool is different. Otolith microchemistry can be used to discriminate between individuals who have resided in different environmental conditions for some part of their lives. The chemical composition of specific life history stages can be isolated and compared between and among groups of fish (Campana et al., 2000). Otolith shape, on the other hand, can be used to reveal the combined effect of genetic, migration and environmental factors on the fish throughout its life (Keating et al., 2014; Vignon and Morat, 2010).

1.4 Stock Assessments

In stock assessments, fisheries scientists attempt to estimate the size of the fish stock and the fishing mortality rate using catch and effort data from the fishery in assessment models to determine biological reference points, for example, maximum sustainable yield (MSY) (Berger et al., 2009; Cooper, 2006). To calculate the reference points, data on the fishery, in terms of catch, effort, fishing mortality, relative abundance and the species' life history are needed. These data can be derived from both fishery dependent (e.g. portside sampling, logbook data, observer data) and independent (research surveys, tagging programmes, mark-and-recapture studies) sources (Berger et al., 2009; Cooper, 2006; Cosgrove et al., 2014c). Fishery independent data are difficult to collect because of the financial obligation required to conduct these surveys and studies. Also for species that are highly migratory or reside over large areas, accumulating independent data may not be feasible (Cosgrove et al., 2014; Maunder et al., 2006). In such cases, fishery dependent data are frequently used; however, the complexity of the data (e.g. differences in fleet behaviour, gear types and vessel size) is an issue. Catch and effort data are standardised to remove the effect of these varying factors so that the data reflects the abundance of the stock (Cosgrove et al., 2014c). Previous studies have identified instances where catch-per-unit-effort (CPUE) estimates from fishery dependent data are not suitable as abundance indices for stock assessments, for example, changes in the environment, fish population dynamics and the behaviour of the fishing fleet (Maunder et al., 2006). To ensure the continued and reliable use of fishery dependent data, as a viable data source for stock assessments, the assumed relationship between catch and effort data and indices of abundance must continue to be examined and improved.

1.5 Fleet Behaviour Dynamics

Understanding how the behaviour of the fleet influences catch and effort data has been an emerging topic in recent years. Using tools from the field of animal movement ecology, such as state-space models and Markovian models, have allowed fishery scientists to infer behavioural states from movement patterns in order to properly define fishing effort (Langrock et al., 2012; Walker and Bez, 2010). For example, authors (Joo et al., 2013), used Markovian models to infer the behavioural states (searching, fishing and cruising) of Peruvian purse-seiners fishing for anchovy, using observer and Vessel

Monitoring Systems (VMS) data. The time periods associated with the vessels' activities can be quantified, which can be used to give more accurate effort estimates when standardising CPUE data. To date, only one study has related VMS adjusted estimates of fishing to catch rates (Charles et al., 2014), therefore, further development is required in this emerging area of study.

A clear understanding of fish species' population structure, especially those that are of high economic importance is critical to its long-term sustainable management. Sustainable management also necessitates the use of appropriate data and tools to carry out stock assessments to ensure management can make informed decisions. The collection of work in this thesis was focused on elucidating the population structure of albacore tuna (*Thunnus alalunga)* in the North Atlantic, as well as modelling fleet behaviour to improve effort estimates used to standardise CPUE.

1.6 Species of Interest

Albacore tuna is one of the most economically important tuna species, and it can be found in tropical and temperate zones of every ocean basin as well as the Mediterranean Sea (Collette and Nauen, 1983; FAO, 2010). It is a highly migratory species that can be distinguished from other tunas by its long pectoral fin. It can reach a maximum length and weight of 127 cm and 40 kg respectively (Collette and Nauen, 1983). The migration patterns undertaken by albacore differ based on age. Juveniles (ages1-4) migrate to temperate regions to feed in the surface waters during the summer. Meanwhile, adults (ages 5-12) travel to deep subtropical waters (250-300 m) to feed and spawn. During the winter, both age groups come together to feed in sub-tropical to tropical waters (Chen et al., 2005; Dufour et al., 2010; Jones, 1991). Albacore tuna are batch spawners with spawning events, releasing over 2 million eggs in an episode (Luckhurst and Arocha, 2015).

1.7 Albacore tuna Management

Due to its economic importance and widespread distribution, stocks of albacore tuna, along with other tunas and tuna-like species, are managed globally by four regional fisheries management organisations (RFMOs). The five organisations consist of countries who have fishing interests in the region. They are: The International Commission for the

Conservation of Tunas (ICCAT); The Inter American Tropical Tuna Commission (IATTC), responsible for stocks in the Eastern Pacific; the Indian Ocean Tuna Commission (IOTC) and Western and Central Pacific Fisheries Commission (WCPFC).

In the Atlantic, ICCAT assumes the existence of three stocks, the North Atlantic, South Atlantic and the Mediterranean Sea. The separation of these stocks is based on inconsistent biological information, in the areas of its genetic framework, migration and spawning locations (Arrizabalaga et al., 2002; Luckhurst and Arocha, 2015; Montes et al., 2012). In the North Atlantic, albacore's population structure is not fully understood (Nikolic et al., 2016), leaving the species susceptible to overexploitation and possible collapse. Various techniques have been used to investigate albacore's structure, such as microsatellites (Davies et al., 2011), otolith microchemistry (Fraile et al., 2016), tagging studies and body morphometrics (Fonteneau, 2010). These studies have indicated that the stock may comprise of multiple subpopulations, but the evidence is not conclusive.

For the management of these stocks, scientists use fishery dependent catch and effort data to carry out stock assessments (ICCAT, 2016). The fishery dependent data are derived from surface and longline fisheries targeting albacore tuna juveniles and adults. The sub-adults and adults are caught mainly by Chinese-Taipei and Japanese longline fleets year-round (ICCAT, 2016; Lehodey et al., 2014). From June to October, Spanish baitboats and trolls, Portuguese baitboats, French and Irish mid-water pair trawls exploit albacore juveniles as they undergo their trophic migration to the waters off the coast of the Azores, in and around the Bay of Biscay and the southwestern waters of Ireland (Bard, 2001; Ortiz de Zárate and Cort, 1998). Irish fishers began targeting albacore tuna in 1990 using drift nets. With the ban on drift nets by the European Commission in 2002, the Irish fishery transitioned to mid-water pair trawling and trolling. Mid-water pair trawling is the predominant method currently used to fish for albacore in Ireland (Cosgrove et al., 2014b). In 2016, the Irish fishery landed approximately 2,300 tonnes valued at 10 million euros (Bord Iascaigh Mhara, 2016).

The albacore stock in the North Atlantic is considered to be marginally overfished but is not presently undergoing overfishing (ICCAT 2016). Therefore, more detailed information concerning albacore's population structure, and data to estimate indices of abundance used in its assessment models are necessary to provide managers with the

knowledge they need to make informed decisions about the welfare of the stock and to prevent the loss the species' genetic and behavioural variability.

1.8 Summary of Objectives

The overall objective of this research was to advance the present understanding of albacore tuna's population structure and to improve fishery-dependent estimates of relative abundance. To address this objective, three studies were conducted using otolith shape analysis, otolith microstructure and microchemistry analyses and hidden semi-Markov models to model fleet behaviour, covered in Chapters 2,3, and 4 respectively.

The aim of the first study (Chapter 2) was to examine spatial variation in otolith shape from catch locations in the North-east Atlantic and to establish if contingents with distinct otolith shapes can be identified and if these attributes can be used to elucidate stock structure. The shape of the otolith was described using Elliptical Fourier harmonics as well as shape and size indices. The variables were analysed using analysis of covariance (ANCOVA) and a generalised canonical discriminant model in order to determine if there were any differences in shape between catch locations.

The second study (Chapter 3) investigated the otolith microstructure and microchemistry of juveniles caught in the Bay of Biscay and adults caught around Canada and Venezuela. The aim of this study was to determine whether or not albacore juveniles and adults share a common environment during their larval or pre-juvenile life stages. For the microchemical analysis, element:Ca ratios were extracted using the laser ablation-inductively coupled plasma mass spectroscopy (LA-ICPMS) technique.

The aim of the third study (Chapter 4) was to investigate the influence of fleet behaviour on catch-per-unit-effort estimates using hidden semi-Markov models and finite mixture models. In the study, hidden semi-Markov models were used to model fleet behaviour from observer and VMS data using vessel speed as the observed variable. Finite mixture models were used to standardise CPUE data and to compare the effect of behavioural variables quantified in the Markovian model. Data from the Irish mid-water pair trawl fishery were used in the study.

An overall discussion chapter (Chapter 5), discussing the key findings of the thesis and suggestions for future studies is also presented.

Chapter 2: Otolith shape analysis as a tool for stock separation of albacore tuna feeding in the North-east Atlantic

2.1 Abstract

For management purposes, albacore tuna (*Thunnus alalunga*) in the North Atlantic is considered to be from one homogenous stock. However, multiple lines of evidence suggest that there is some degree of stock complexity. In this study, the stock structure of North Atlantic albacore tuna is investigated using otolith shape analysis. Juvenile albacore tunas were collected from the commercial fishery in the Bay of Biscay region over a three-year period (2012-2014). Catches were concentrated in two main areas: within the Bay of Biscay (East) and off the western shelf edge (West). Otolith shape was defined using Elliptical Fourier analysis and was compared between albacore from these two catch locations using generalised canonical discriminant analysis. The results show significant differences in otolith shape between albacore from the Eastern and Western locations using Elliptical Fourier descriptors. The discriminant analysis and jack-knifed cross-validation classification correctly classified East and West samples with a success rate of 72% and 75% respectively. The results suggest that two components with distinct environmental life histories contribute to the fishery in the North-east Atlantic. It also implies that albacore juveniles display some degree of fidelity to their feeding areas.

2.2 Introduction

Albacore tuna (*Thunnus alalunga)* is a highly migratory fish found in the tropical and temperate waters of every ocean basin (Arrizabalaga et al., 2015; Collette and Nauen, 1983). For management purposes, albacore tuna in the Atlantic Ocean are divided into three stocks: North Atlantic, South Atlantic, and the Mediterranean. The separation is based on limited knowledge of spawning locations, spatial distribution of different life stages, movements of tagged fish, and observed morphometric variations (Arrizabalaga et al., 2004; Cosgrove et al., 2014a; ICCAT, 2011; Montes et al., 2012).

The life cycle of North Atlantic albacore tuna is not well understood; however, it is assumed that adults and juveniles spend winter in the central Atlantic (Santiago and Arrizabalaga, 2005). At the beginning of summer, both adults and juveniles begin their separate migrations. The adults migrate to the warm waters of the southern Sargasso Sea to spawn from about 5 years old (Luckhurst and Arocha, 2015). Juveniles (Ages 1-4) migrate to their feeding grounds in the Azores, south-west Ireland and the coastal and offshore waters of the Bay of Biscay (Sagarminaga and Arrizabalaga, 2014; Santiago and

Arrizabalaga, 2005). It has been proposed that they follow two potential routes to this area: the Azorian - from the Azores to the offshore waters of the Bay of Biscay and the Celtic Sea, and the Cantabrian - from the coastal waters of the Iberian Peninsula to the inner Bay of Biscay (Hue, 1980).

These different migration routes might correspond to different subpopulations. In fact, the subpopulation structure of albacore tuna in the North Atlantic is not fully understood (Nikolic et al., 2016). Various approaches have been used to investigate its structure, such as microsatellites (Davies et al., 2011), otolith microchemistry (Fraile et al., 2016), tagging studies and body morphometrics (Fonteneau, 2010). These studies have indicated that the stock may comprise multiple subpopulations, but the evidence is not conclusive. For example, in the Bay of Biscay and Celtic Sea, differences have been found in the juveniles' spatial distribution. There is evidence of distinct groups feeding in the offshore and inshore waters of the bay (Fraile et al., 2016; Sagarminaga and Arrizabalaga, 2010). It has also been suggested that stock composition in the Bay of Biscay may vary throughout the season as juvenile albacore from different areas migrate to feed (Davies et al., 2011).

Fisheries have been able to target this species at their feeding grounds because of their predictable migration pattern and the propensity of juveniles to feed in surface waters (Goñi et al., 2011; Goñi and Arrizabalaga, 2010). The fishing season is from June to October and it consists of Irish, Spanish, French and Portuguese surface and mid-water fishing boats. For the period 2010 to 2014, surface fisheries (baitboat and trolling) accounted for approximately 65% of the total catch in this area (ICCAT, 2016). If population structure is not accounted for in stock assessment and management initiatives, less productive components could be overfished and the genetic and/or behavioural variability of the stock could be lost (Benzinou et al., 2013). These subpopulations may have different spawning origins or may inhabit environments with different physical oceanographic characteristics e.g. temperature or salinity (Fraile et al., 2016; Wright et al., 2002). Such differences could produce variations in phenotypic traits such as otolith shape.

Otolith shape analysis has been found to be an effective tool in detecting inter- and intra-specific differences originating from genetic and environmental influences (Schulz-Mirbach et al., 2008; Stransky, 2013; Vignon and Morat, 2010). Otolith shape has been

used to discriminate between stocks of various species (Leguá et al., 2013; Petursdottir et al., 2006; Stransky et al., 2008b; Tuset et al., 2003). Several techniques are available to describe the otolith shape such as biorthogonal grids, Euclidean distance matrix analysis and various types of Fourier functions (Tracey et al., 2006). Elliptical Fourier functions use harmonics to describe the shape of the otolith. The amplitude of each harmonic represents a shape characteristic e.g. elongation and triangularity (Bird, 1986). This method has been used substantially in recent studies and has shown to be proficient at distinguishing groups with subtle otolith shape differences (Benzinou et al., 2013; Galley et al., 2006; Stransky et al., 2008a).

The classic approach to characterise a stock is to acquire samples during a spawning event and use those attributes to determine the composition of a mixed assemblage. But, in the case of albacore, fisheries do not target spawning aggregations, making it difficult to sample spawning adults (Luckhurst and Arocha, 2015). Therefore, in this study, a top-down approach was applied to a potentially diverse aggregation in an attempt to identify components within it. The aim of this study was to examine spatial variation in otolith shape from catch locations in the North-east Atlantic and to establish if contingents with distinct otolith shapes can be identified and if these attributes can be used to elucidate stock structure. The otolith shape was described using Elliptical Fourier functions along with shape and size indices.

2.3 Methods and Materials

2.3.1 Fishery data

Geographic location of albacore catches in the Bay of Biscay region were extracted from logbooks for the fishing seasons of 2012 to 2014. The catch locations of fishing vessels from which albacore tuna heads were collected were mapped using ArcGIS ArcMap 10.2. Catch locations were separated into two groups. Following Fraile et al. (2016) and Sagarminaga and Arrizabalaga (2010), albacore catches from west of the 10°W meridian were classified as “West” and catches from east of the 10°W meridian were classified as “East” (hereafter called West and East respectively) (Fig. 1). For each sample, the total length (cm), weight (kg), date of catch and the fishing vessel was also recorded. The sagittal otoliths were removed, cleaned, air dried and stored in individually labelled plastic tubes. For this study, only otoliths from fish whose total fish length was between

50 cm and 87 cm were used to ensure all samples were restricted to the juvenile stage. This length range corresponds to albacore aged between 1-4 years old (Ortiz de Zárate et al., 2013; Santiago and Arrizabalaga, 2005). After the visual inspection, 67 samples were used in total, 43 samples caught in the East and 24 in the West (Table 1).

2.3.2 Shape analysis

Otoliths were photographed using a stereomicroscope (Olympus SZX10) connected to a digital camera (Q Imaging Retiga 2000R) with a PC interface. No broken otoliths were not used in the analysis. Both left and right otoliths were photographed, and their images were rotated to an assigned position. Images were converted to 8 bit and the otolith outline was selected by intensity thresholding in Image J (Version 1.48) (Fig. 2). The selection was used to measure 8 size (area, perimeter, major and minor Feret's diameter, height and width of the bounding rectangle and major and minor axes of an ellipse) and 4 shape indices (circularity, aspect ratio, roundness, solidity). Three additional shape variables were calculated for each otolith, form factor, (4π*area/ (perimeter)^2), ellipticity, ((*Feret length – Feret width) – (Feret length + Feret width))* and squareness, *(area / (Feret length x Feret width))*. Otolith outlines were saved as XY coordinates for subsequent extraction of Elliptical Fourier coefficients.

2.3.3 Elliptical Fourier analysis

Elliptical Fourier analysis was conducted using the R statistical program (Version 3.2.3). Using the Momocs package (Version 0.9.63), the coordinates of each otolith were scaled and smoothed. A Fourier power test was performed, and the first twelve harmonics were shown to describe 99% of the cumulative variability of the otolith shape. Each harmonic consists of four coefficients; thus 48 coefficients were produced for each otolith. Three coefficients in the first harmonic were used to standardise for orientation, rotation, and size, leaving 45 coefficients. Combining the Elliptical Fourier coefficients and the otolith morphometric variables produced 60 variables (8 size and 7 shape parameters, 45 Fourier descriptors) including fish length.

2.3.4 Statistical analysis

Using the growth curve from Santiago and Arrizabalaga (2005), the age of the fish samples was estimated. The mean fork length value for the catch locations was calculated and their frequency distributions were plotted. All the variables were tested for normality and homogeneity of variance using the Shapiro and Levene's test respectively and were transformed when necessary. Correlations between fish length and each variable were tested using Pearson's correlation statistic. Variables significantly correlated with fish length were standardised using the common within-group slope from an analysis of covariance (ANCOVA) with location included as a factor and fish length as a covariate (Tracey et al., 2006). A significant interaction term indicated that the relationship between fish length and the variable was not consistent across locations and the common within-group slope could not be used to standardise for the effect of length; these variables were thus omitted. After the standardisation of 22 variables (9 size and shape indices, 13 Fourier coefficients), the ANCOVA was rerun. Variables that differed significantly by location were considered potentially useful and were chosen for further analysis.

A correlation plot was produced to determine if any of the selected variables were correlated with each other. If two variables were correlated ($r^2 > 0.5$), one of the variables was randomly chosen for omission. Based on the results of the tests, five Fourier descriptors (C5, C11, D3, D7 and D12) were selected. Descriptors D3 and D7 were corrected through a Box-Cox power transformation for normality and homogeneity of variance respectively. Descriptor D12 was correlated with fish length and was corrected with the common within-group slope. Because of the nature of the fishery, an uneven number of samples were collected for each year and from each area (Table 1). Ideally, an equal number of samples should be collected from each area for each year to ensure the differences observed in the data are not skewed by other effects such as interannual variability. However, this was not possible in our study which relied on samples from the commercial fishery.

To ensure the variation observed in otolith shape was not a result of interannual variability, the data were separated into two groups and univariate analyses of variance (ANOVAs) were carried out on the descriptors in each group. The first group contained the samples caught in the East during the three-year period and was used to assess the strength of the year effect. The second comprised of the samples caught in both areas in

2014 and was used to determine the strength of the location effect. The coefficient of determination (or r^2) and the p-value were recorded for each descriptor in both groups. If the r^2 values of the first group were greater, then the significance of the descriptors was a result of a year effect. If the second group had larger r^2 values, then the significance of the descriptors was due to a location effect. A generalised canonical discriminant analysis was performed using the selected variables to identify differences in otolith shape between albacore caught in the two areas. Jack-knifed cross-validation procedures were conducted to calculate an unbiased evaluation of classification success. The Meanshapes function in Momocs was used to recreate the shape of the otolith for both locations using all the samples and only the otoliths collected in 2014.

2.4 Results

Based on the five Fourier descriptors, the mean and variance of the East otoliths were significantly different to the West otoliths. The descriptors were from the low and middle-level harmonics suggesting that the dissimilarities were in both the gross shape and the finer details of the otolith. Of the five descriptors, D12 was the most important in discriminating between fish from the two areas followed by C5, D3, C11 and D7 (Table 2). All five descriptors, except D7 and C11, were strongly correlated to the first canonical discriminant and were considered important in discriminating between fish from the two areas (Table 2).

The canonical discriminant analysis revealed a separation between the two groups along the first discriminant (p-value = 0.002). The two groups showed significant differences in their canonical scores but with a region of overlap (Fig.3). The dissimilarities between the two groups are captured in the plots of the mean otolith shape for all the samples and the 2014 samples (Fig.4). The East otoliths possess a narrower rostrum and the West has a slightly broader post-rostrum. Also, despite the small East sample size, the 2014 mean otolith shape showed some shape differences between the two locations. Using all five descriptors, the classification score for the discriminant analysis was 72.1% in the East and 75% in the West (Table 3).

The ages of the juvenile albacore used in this study ranged from 1 to 4 and all ages were detected at both locations. The fork length frequency distributions were found to be similar with Eastern samples having a slightly larger range than the Western samples (X-

squared = 11.92, p-value = 0.06) (Fig. 5). There was a small difference in mean fork length between the two areas, (West = 73.8 cm, East = 70.2 cm) which was not significant. The assessment for interannual variability of the East samples showed that none of the descriptors were different between the years. The location effect observed in the samples collected in 2014 was difficult to detect because of the small sample size (Table 1). Only the C11 descriptor (p-value =0.035) was found to be significantly different between the samples caught at the two locations in 2014 (Table 4).

2.5 Discussion

The aim of this study was to examine the spatial variation in otolith shape between albacore tuna caught at two separate locations. Despite our small sample size, the results from the Fourier and discriminant analyses clearly show that the average otolith shape changes based on catch location (Fig. 4). The selected variables were also able to discriminate between the East and West locations with a classification success of 72% and 75% respectively to *a priori* grouping. This can occur if the distributions of two stock subpopulations at the feeding area overlap partially, as suggested by tagging data (Arrizabalaga et al., 2002), but not completely. Alternatively, misclassification may reflect a degree of similarity in the otolith shape of fish from two entirely distinct stock components.

Our results have identified differences between albacore caught in and around the Bay of Biscay. We propose that they have most likely accumulated over the life of the fish and may represent different life histories. Although these dissimilarities cannot be used to discriminate between the two locations completely, the observed variation in shape indicates that albacore caught in the East has a different environmental life history to the fish caught in the West. Also, our conclusions add validity to the hypothesis that different contingents migrate to feed in the North-east Atlantic (Aloncle and Delaporte, 1974; Bard, 2001; Fonteneau, 2010; Fraile et al., 2016). Altogether, these results add to a growing body of evidence that supports stock complexity in this region (Nikolic et al., 2016).

It must be noted that in the West there were a small number of samples with fork lengths between 50 – 60 cm. Juveniles in this length range would have undergone fewer migrations than larger individuals, resulting in a difference in their migration histories.

This difference could have played a role in the otolith shape dissimilarities observed between the two locations; however, any differences in size or length would have been dealt with by standardising for size effects in the creation of the Fourier descriptors and by using the common within-group slope to remove any correlations with length.

Due to restrictions on the collection of samples from the commercial fishery, the sampling was not balanced; samples from the East were collected in 2012, 2013 and 2014 while in the West only samples from 2014 were available. Therefore, the possibility that the shape differences observed may be confounded by interannual variability was investigated. It must be noted that after dividing the data, the sample size of both groups was small and therefore the results should be interpreted with caution. The univariate ANOVAs showed that in the samples from the East, none of the shape variables varied between years. With the samples collected in 2014, it was difficult to detect the location effect using the small sample size available; however, a small effect was observed with descriptor C11. This indicates that the observed variation in otolith shape is unlikely to be an artefact of the sampling design.

Population structure in the North-east Atlantic has been studied for many years using various genetic, otolith microchemical and microstructural techniques. The genetic investigation into the separation of albacore tuna in the North Atlantic is inconsistent at best. According to Davies et al. 2011, genetic heterogeneity and spatial structuring were observed within the North Atlantic stock using microsatellite analysis. The authors stated that divergence was seen between the Bay of Biscay and the Celtic and western Ireland samples. The spatial variation observed was separated by the 10°W meridian, similar to our study. However, a recent multiannual genetic study, using larger samples sizes and single nucleotide polymorphisms (SNP), showed that the North Atlantic was a homogeneous stock (Albaina et al., 2013; Laconcha et al., 2015). Using the laser ablation inductively coupled plasma mass spectrometry (LA/ICP-MS) technique, Fraile et al. (2016) analysed albacore tuna otoliths collected from in and around the Bay of Biscay, separating the samples based on capture location east and west of the 10° W meridian. The authors found no evidence that the juvenile albacore tunas had different larval origins. They did, however, find that the Sr:Ca concentrations in the post-core region of the otolith were significantly different between the two groups implying that the individuals occupied different areas during their early years. They also suggested that

albacore collected in the East began migrating to the North-east Atlantic feeding area at an earlier age (age 1) while individuals caught in the West began at a later age.

Currently, albacore tuna in the North Atlantic is managed as one homogenous stock. Our study shows that there is some complexity within the mixed aggregation of albacore feeding in the North-east Atlantic. To produce the difference in otolith shape observed in this study, albacore juveniles caught at the two catch locations could be from the same spawning area but have different migration routes or they could be from two distinct spawning areas that make similar migrations during the summer to feed. If they are of separate spawning origins, this will have serious implications for the assessment and management of the stock. If they are from the same spawning area but with significantly different life histories, then depending on fishing effort, which varies from year to year, one group may be targeted more than the other. This can have a large impact on within-stock diversity (e.g. variability in life-histories, behaviours, migration patterns), with potential consequences for stock resilience and stability (Kerr et al., 2010a).

In our study, a top-down approach was utilised, that instead of collecting samples during a spawning episode, they were gathered from mixed feeding aggregations. The top-down approach has been used in studies on various marine species such as hawksbill (Monzón-argüello et al., 2010) and loggerhead turtles (Monzón-argüello et al., 2009) and blue whiting (Giedz, 1982). This approach can be used to gather initial insights into an organism's genetic composition (Monzón-argüello et al., 2010), to assess spatial variation in juvenile mixed aggregations (Monzón-argüello et al., 2009) or to determine a population's structure based on morphometric and meristic measurements (Giedz, 1982). The results of our study, as well as, the ones mentioned above, demonstrate that this approach is worthwhile especially if insufficient information is known about the species' population in an area or if spawning sites are unknown or undefined.

Future work should focus on characterising the source of variation in shape observed in albacore juveniles feeding in and outside the Bay of Biscay. They should incorporate genetic, microchemical and microstructural techniques to ensure a holistic approach is utilised to effectively characterise the stock. Markers of larval origin (otolith core chemistry, microstructure, genetics) could be used to determine if the fish are from different spawning areas, while analysis of chemical composition or growth marks along the otolith transect could help to establish if they have occupied different environments

later in life. Spatial and temporal control is an important aspect of sampling. While the use of the commercial fishery allows for the cost-effective collection of samples, spatial and temporal parameters are less controlled. To reduce the dependence on the commercial fishery, a targeted sampling program is needed, especially in and around the Bay of Biscay, where differences in otolith shape and microchemistry are being observed (Fraile et al., 2016). Tagging studies of juveniles feeding in the two locations may prove to be vital in improving our understanding of albacore tuna life history outside of the Bay of Biscay region (Childers et al., 2011; Prince et al., 1995).

In conclusion, otolith shape analysis has been demonstrated to be an effective tool at distinguishing juvenile albacore tuna feeding in and outside the Bay of Biscay. Otolith shape analysis is a cost-effective and quick method which can be used as an additional method to complement other discriminating methods in the pursuit of understanding the population structure of the North Atlantic albacore tuna stock.

Table 2. 1 Juvenile albacore sampled per year, including average length (cm) and capture location

Location	Year	Quantity	Mean Length ± SD (cm)	Total
East	2012	18	66.1 ± 11.9	--
	2013	16	75.4 ± 11.2	--
	2014	9	70.1 ± 11.9	43
West	2014	24	72.0 ± 10.4	24

Table 2. 2 Results from the structure matrix of the standardized canonical coefficients, ordered by size of correlation within the function.

Fourier descriptors	FDA 1
D12	0.563
C5	0.483
D3	-0.338
C11	-0.318
D7	-0.286

Table 2. 3 Jack-knifed cross-validation matrix showing the percentage of correct classifications derived from discriminant analysis

	East	West	Percentage
East	31	12	72.1
West	6	18	75.0

Table 2. 4 The results from the test for interannual variability using samples collected in the east over the three-year period (2012-2014) and samples collected from both locations in 2014.

Year effect	R^2 value	p-value
C5	0	0.998
C11	0	0.782
D3	0.006	0.337
D7	0	0.411
D12	0.014	0.286

Location effect	R^2 value	p-value
C5	0.034	0.154
C11	0.107	0.035
D3	0	0.799
D7	0	0.599
D12	0.006	0.284

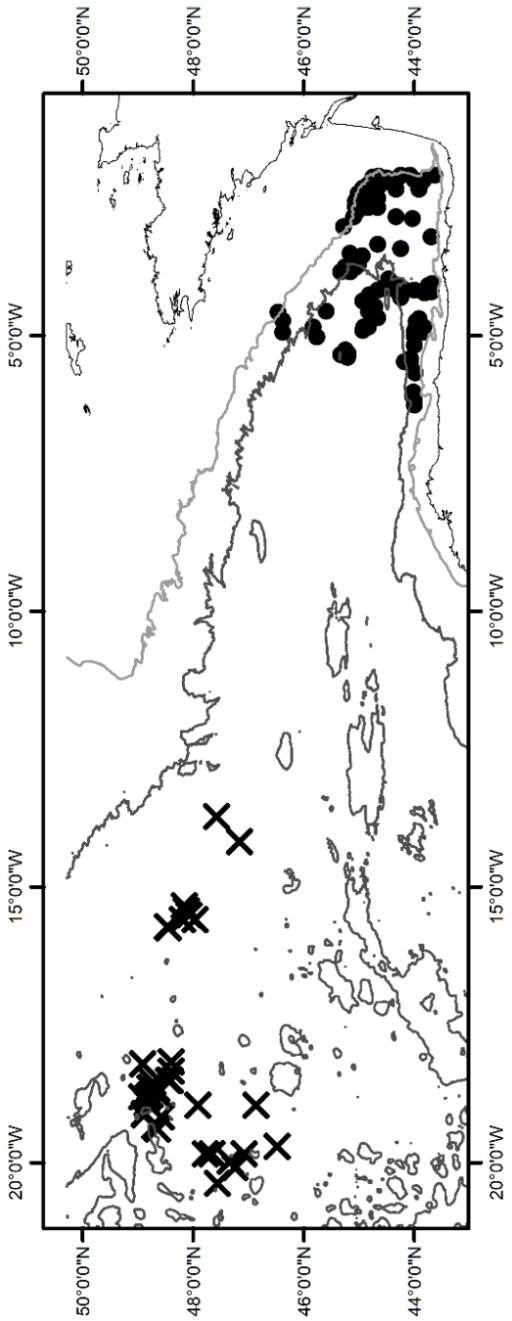

Figure 2. 1 Catch locations of juvenile albacore in and outside the Bay of Biscay. Map source: WGS84, 200 m (light grey) and 4000 m (grey) depth contour shown, Scale: 1 cm = 148 km. The symbols, X and ● represent the catch locations west and east of the 10°W meridian respectively.

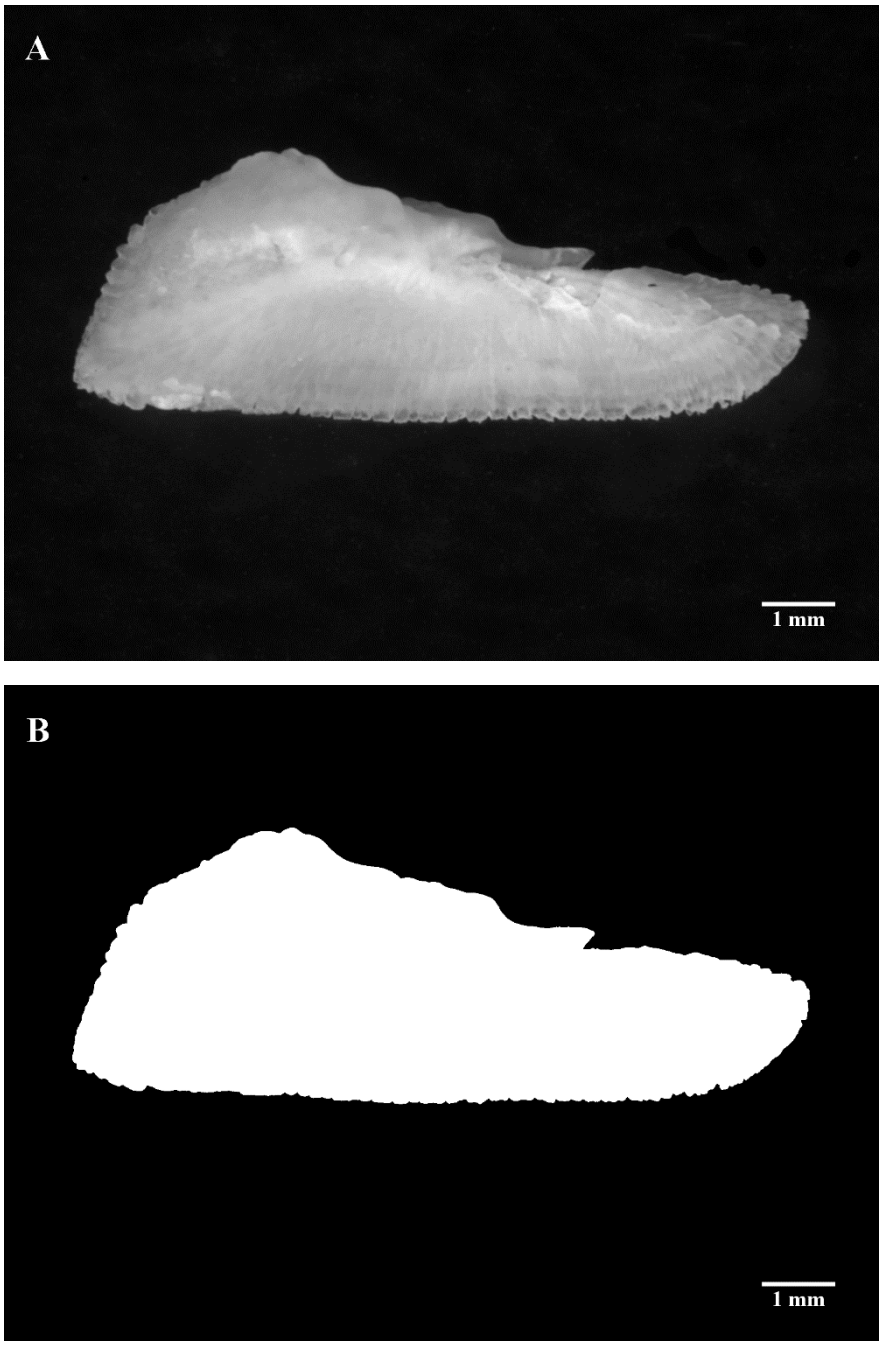

Figure 2. 2 Albacore tuna left otolith before and after image processing. (A) The original image before intensity thresholding, (B) The modified binary image before a selection is created.

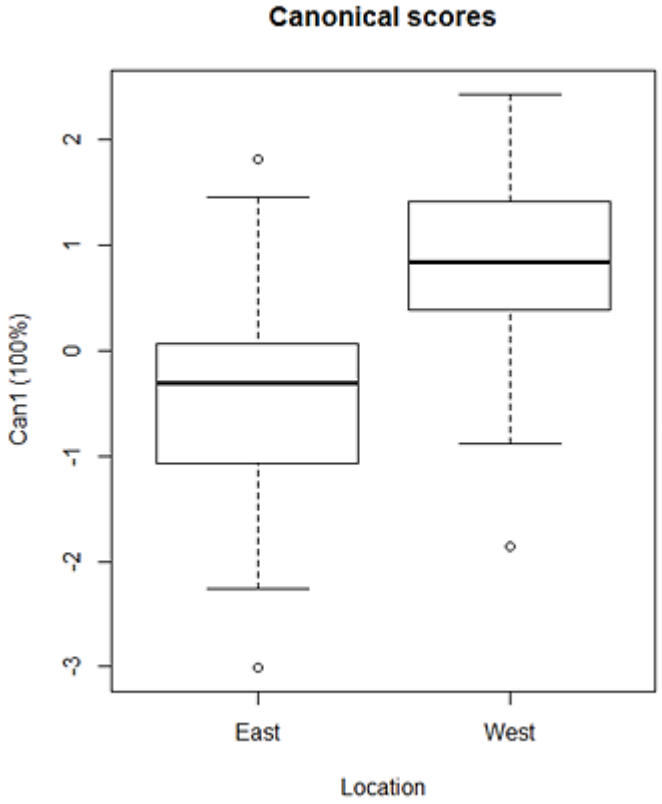

Figure 2. 3 Parallel boxplots of the Canonical scores for albacore caught in each catch location.

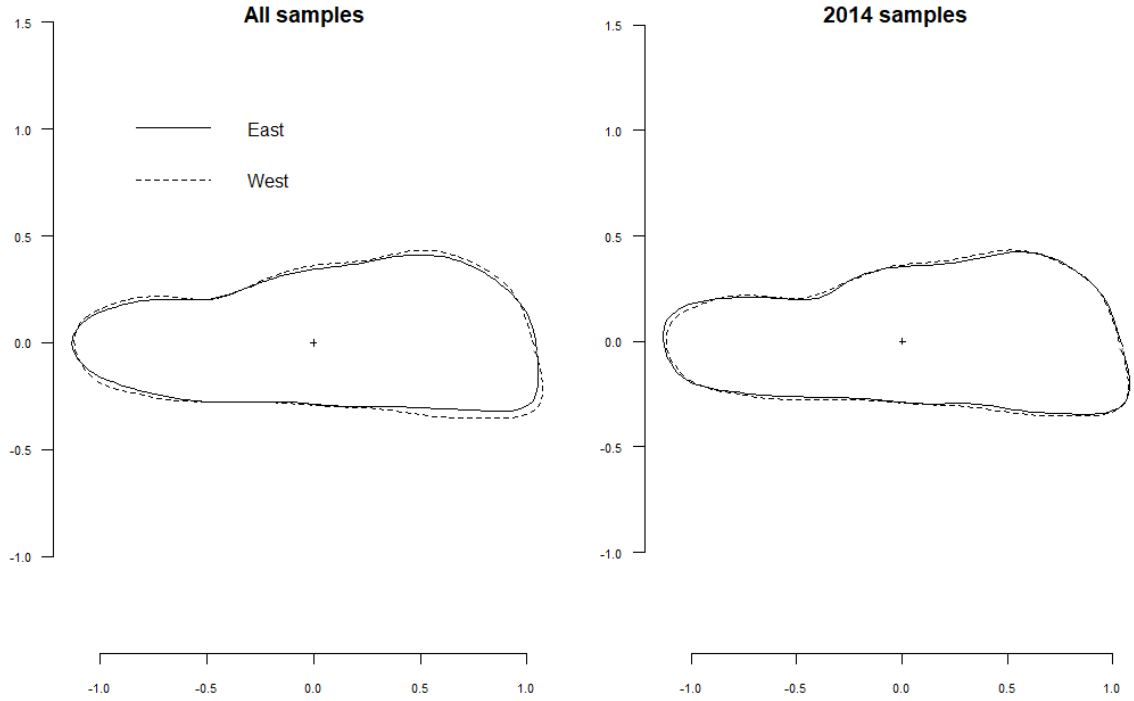

Figure 2. 4 Mean shapes of albacore tuna by catch location for all samples and for 2014 samples.

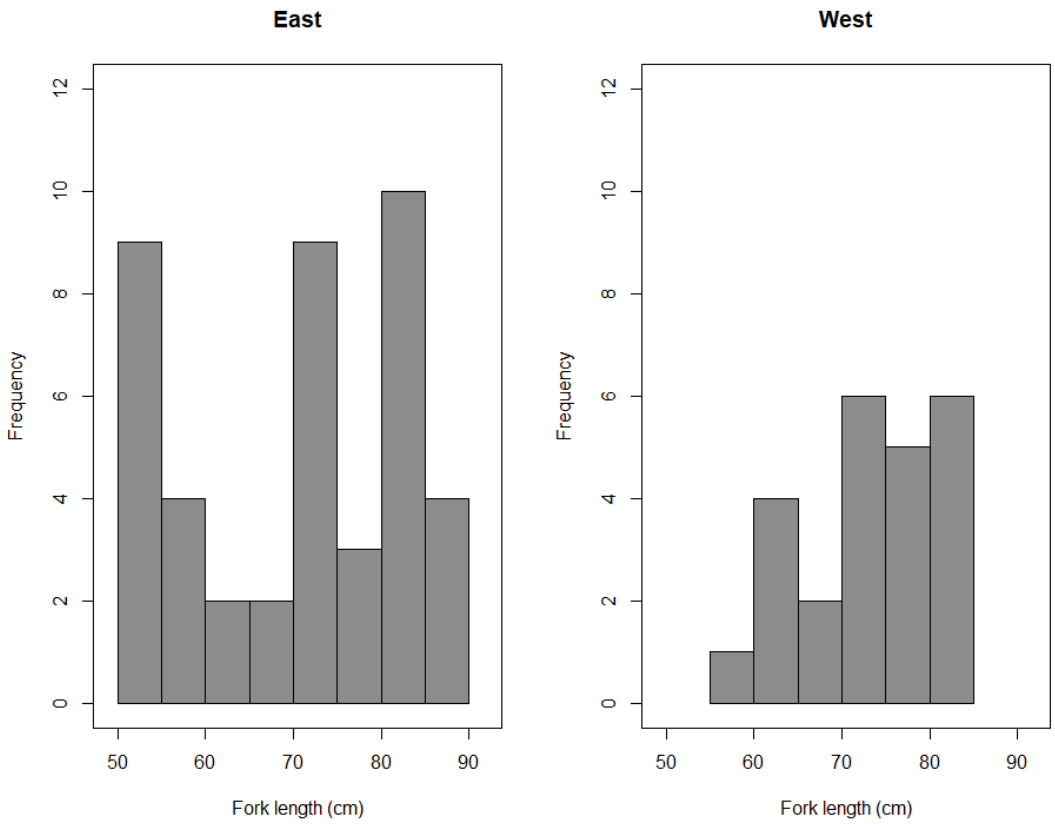

Figure 2. 5 Fork length frequency distribution categorised by catch location.

Chapter 3: Investigation into North Atlantic albacore tuna, (*Thunnus alalunga)* larval life history using otolith microstructure and microchemistry analyses

3.1 Abstract

Little is known about the early life history of albacore tuna in the North Atlantic. In this study, the pre-juvenile life stage was investigated indirectly using otolith microchemistry and microstructure analyses. Juvenile albacore tuna was caught from surface fisheries located in the Bay of Biscay and adults were collected from recreational and longline fisheries operating offshore of Canada and Venezuela. All fish used in the study were from the 2007 or 2008-year classes. For the microstructure analysis, the larval increment widths of the first 12 growth rings were measured and increment widths were compared between locations. Element:Ca otolith ratios, extracted from two areas (the core and post-core) on the growth axis, were quantified for ten elements, Li, Mg, Mn, Fe, Co, Cu, Ni, Zn, Sr and Ba. Both analyses were conducted to discern whether or not the juveniles and adults shared a common larval or pre-juvenile environment. The microstructure analysis showed that albacore from the three locations did not display significantly different larval growth rates. However, differences in the microchemistry of the larval core were evident. It was possible to separate the samples into two groups indicating that there may be more than one spawning location present in the North Atlantic. There was a high degree of overlap in the post-core concentrations indicating a convergence of life-histories during the early juvenile phase.

3.2 Introduction

Otoliths are calcium carbonate and protein structures located in the inner ear of all teleost fish (Morales-Nin, 2000). They accrete throughout the life of the fish and are never reabsorbed (Campana et al., 2000). The chemical composition of otoliths reflect the physicochemical characteristics of the surrounding environment, even though they are regulated by biological processes (Campana et al., 2000; Geffen and de Pontual, 2002). The information stored in otoliths can be used to reconstruct early life histories of widely distributed species; especially those that are difficult to sample. Otolith microstructure analysis has generally focused on assessing fish age and growth rate (Chen et al., 2012; Pepin et al., 2001; Wells et al., 2013). It is also used to identify development stages, such as hatch time and metamorphosis (Baumann et al., 2015; Toole et al., 1993). Otolith microchemistry can be used to reconstruct fish movement patterns (Elsdon et al., 2008),

identify spawning areas (Rooker et al., 2014) and discriminate fish populations (Campana et al., 2000).

Albacore tuna is a temperate pelagic species and an important food source globally (FAO, 2010). It is one of the most economically important tuna species and is found in every ocean basin (Collette and Nauen, 1983; FAO, 2010). In the Atlantic, ICCAT assumes the existence of three stocks (the North, South and Mediterranean), based on knowledge about spawning areas, distribution of fisheries, tagging and genetic studies (Arrizabalaga et al., 2004; Bard, 1981; Fraile et al., 2016; Montes et al., 2012; Nikolic et al., 2016).

Little is known about the early life stages of albacore tuna in the North Atlantic; larval distributions are not well described and the general life cycle is uncertain (ICCAT, 2011; Ortiz de Zárate et al., 2004), but it is assumed that they spawn in the southwestern corner of the North Atlantic (Figure 3.1). Albacore tuna are batch spawners with spawning events occurring from April to September with a peak in the month of July (Luckhurst and Arocha, 2015). The larval stage is short in duration and the juvenile stage begins at approximately 2 cm (Bard, 1981). After 40 cm (age 1), juveniles are exploited by surface fisheries in the North-east Atlantic. Below 40 cm, albacore tunas are rarely caught by commercial or recreational means. In the Caribbean, artisanal fisheries have been known to catch albacore below 40 cm; however, because of a lack of knowledge or interest in the fishery in this area, many albacore samples are either misidentified or under-reported (F. Arocha, personal communication, September 8, 2017). Overall, there is very little verifiable information available about this life stage period (ICCAT, 2011) (Figure 3.1).

During the month of May, juvenile tunas begin their trophic migration to the Bay of Biscay and the south-west of Ireland to feed on anchovy *(Engraulis encrasicolus)* and various crustaceans until October when they return to the central Atlantic to winter (Goñi et al., 2011; Sagarminaga and Arrizabalaga, 2014) (Figure 3.1). Because of their predictable movements, fisheries from different countries have been able to exploit this pelagic resource. Juvenile albacore migrating to the North-east Atlantic are targeted by surface fishing vessels from Spain, Portugal, France and Ireland (Cosgrove et al., 2014c; Goñi et al., 2011). In the summer, adults begin their reproductive migration to different areas in the western Atlantic. The spawning sites in the North Atlantic are not clearly defined (Le Gall, 1974). Previous studies have identified different potential spawning areas based on several lines of evidence. These are in the offshore waters of Venezuela

(where larvae have been recorded) (Ueyanagi, 1971), the southern Sargasso Sea (where temperatures are within the optimum range for spawning) (Luckhurst and Arocha, 2015) and the eastern Atlantic (where adults at late stages of gonadal development have been caught) (Ortiz de Zárate et al., 2004).

Adults are targeted by longline fisheries operating in the central and north-western Atlantic (ICCAT, 2016) and occur as bycatch in the Venezuelan pelagic longline fishery for yellowfin tuna (Arocha et al., 2017). In the western Atlantic, during the summer, albacore migrate into Canadian waters to feed on anchovy, *(Engraulis spp.)*, mackerel *(Scomber spp., Trachurus spp.)*, sardine *(Sardina pilchardus, Sardinops sagax)* and squid. Georges Bank, in particular, is an important foraging area for albacore tuna (Fisheries & Oceans Canada 2011) (Figure 3.1). Earlier studies, using catch locations (Sagarminaga and Arrizabalaga, 2010), microsatellites (Davies et al., 2011), otolith microchemistry (Fraile et al., 2016) and shape analysis (Duncan et al., 2018) have provided evidence to suggest that there may be sub populations present in the North Atlantic stock, particularly in the Bay of Biscay. It is not known if these juvenile sub-populations originated from different spawning sites and if as adults, they return to natal areas to spawn.

From 2012 to 2016, surface fisheries, which target juvenile and subadult fish (50-90cm) account for approximately 80% of the total catch of albacore tuna. The remaining 20% is caught by longline fisheries, which target adult fish (ICCAT, 2016). Although the North Atlantic stock is considered to be marginally overfished but not undergoing overfishing, there are important uncertainties around the present stock status (ICCAT, 2016). With such a strong fishing pressure being exerted on the juvenile and sub-adult life stages and with virtually no knowledge concerning the larval and early juvenile life stages, the probability of overexploiting this stock is high.

There are currently no directed scientific surveys for larval albacore tuna. Most of the commercial fishery is concentrated outside of the spawning season making it very difficult to collect information about the distribution of spawning adults or the location of spawning grounds. However, information stored in the larval core of tuna from the main fishing areas may offer some insight into the early life history and stock structure of the species. In this study, otolith microstructure measurements and otolith microchemistry concentrations from the larval core of juvenile and adult fish were used

to determine whether or not albacore from three fishing areas (Bay of Biscay, Canada and Venezuela) have originated from a common larval and pre-juvenile environment. The results are interpreted in relation to current understanding of albacore stock structure and migrations between spawning and feeding areas.

3.3 Methods and Materials

Otoliths from juvenile albacore were collected from Spanish surface fishing vessels operating in the Bay of Biscay. Adult otolith samples were obtained from two areas fished by the Venezuelan pelagic longline fleet, the southeastern Caribbean Sea and the Guyana-Amazon Atlantic. The Canadian samples were acquired from fishing vessels participating in the annual Wedgeport tuna tournament in Nova Scotia Canada (Figure 3.2). Ages of the samples were estimated from fork length using the growth curve created by Santiago and Arrizabalaga (2005). All of the samples used in the study were from cohorts 2007 and 2008, with a similar number of samples from both cohorts (Table 3.1). The sagittal otoliths were removed, cleaned with deionised water, dried under a laminar flow clean air hood and stored in individually labelled plastic tubes.

Moulds were then coated with Buehler release agent (Buehler Ltd, Lake Bluff, IL, USA) and allowed to dry before the resin solution (EpoThin 2, Buehler Ltd) was added. The otoliths were added to the mould when the solution was firm to ensure the otoliths didn't sink to the bottom of the mould. More solution was added to the mould to ensure the otolith was fully embedded in resin. The moulds were then placed in an oven to cure for 2 hours. After curing, the otoliths were cut transversely using a Buehler Isomet Low speed saw with Buehler IsoCut fluid as a blade lubricant. After cutting, each otolith section was stored in an acid-washed plastic tube. Transverse sections were glued, using Crystal Bond, to a sanding platform. The section was polished with sandpaper of different grit sizes (1200µm, 1500µm, 2000µm, 2500 µm and 4000µm) and distilled water until the primordium was visible under a light microscope (Olympus BX51TF). The section was then removed from the platform, washed with deionised water and stored in a plastic tube. Altogether, 127 sectioned otoliths were prepared for otolith microchemical and microstructural analyses.

3.3.1 Otolith microchemistry analysis

In preparation for the trace element analysis, microscope slides were marked with a glass scriber, broken to a length of 50 mm and covered with double-sided tape. Between 25 - 30 randomly chosen sections were attached to each slide. The analysis was conducted at the Geochronology and Isotope Geochemistry Research Facility (SGIker) of the University of the Basque Country (UPV-EHU) using a laser-ablation inductively coupled plasma mass-spectrometer (LA-CP-MS). The system consisted of a Thermo Fisher iCAP Qc quadrupole mass spectrometer, coupled to a New Wave Nd:Yag 213 nm laser system with an additional vacuum pump to increase the system's sensitivity. Two spots of 55µm diameter were laser ablated on each otolith. The spot size was chosen to ensure adequate resolution and stability of the signals.

The first ablation spot position was set at the primordium, which will be referred to as the core, followed by another spot position at 200µm from the primordium, referred to as the post-core (Figure 3.3). The approximate age of the tuna larvae at each ablation point was estimated using the otolith radius-age relationship, created by Garcia et al. (2006), for larvae spawned in the Mediterranean since there isn't an otolith radius-age relationship for albacore spawned in the North Atlantic. The approximate age at the time the material at the core was deposited was calculated to be between 0-8 days and between 20-36 days for the post-core position. Concentrations were recorded for ten elements: Lithium (^{7}Li), Magnesium (^{25}Mg), Manganese (^{55}Mn), Iron (^{56}Fe), Cobalt (^{59}Co), Nickel (^{59}Ni), Copper (^{64}Cu), Zinc (^{65}Zn), Strontium (^{88}Sr) and Barium (^{138}Ba). Elemental concentrations were recorded in parts-per-million (ppm) and were expressed as ratios relative to ^{44}Ca by using the below equation adapted from Baumann *et al.* 2015. Element:Ca ratio (µmol mol^{-1}) =

$$\left(Molar\ mass\ of\ the\ Element\ (ppm) * \frac{0.40}{Molar\ mass\ of\ Calcium}\right)$$

For each spot, only stable sample signals were utilised in the data treatment process, signals from surface contamination and fractures were omitted. The glass standard, NIST 612 SRM (US Department of Commerce) was used to account for the system's sensitivity and precision as well as instrumental drift. It was measured, in triplicate, after every three otolith sections. Triplicate measurements of a carbonate standard, MACS-3 (pressed powder pellet), provided by the US Geological Survey, was used as a quality control for the results and was measured at the beginning and end of each analytical session or if the

microscope slide was changed during a session. Data were processed using the data reduction software Iolite (Version 3.32). Since Calcium was assumed to be distributed throughout the whole otolith at a concentration of 40%, it was used as an internal standard to correct variations in ablation yield and counting efficiencies. The limit of detection (LOD) for each element was calculated using the mean of the blank signal and three times the standard deviation. The mean values of the Relative Standard Deviation (or RSD) for the NIST 612 and MACS 3 were based on 44 and 5 triple replicate measurements respectively and was used to demonstrate the precision level of the machine. The analytical accuracy was calculated as the observed value⁄ theoretical reference value in percentage (Table 3.2).

3.3.2 Statistical analysis

Statistical analysis of the trace element data was conducted using R (Version 3.3.3). Prior to analysis, the trace element variables were separated by spot position and natural log-transformed to ensure they met the normality assumptions. Concentrations greater than three times the interquartile range from the median of each trace element were considered outliers and were omitted from further analysis. A correlation plot was created to identify multicollinearity between the variables. If two variables were strongly correlated ($r^2 > 0.8$), one was omitted. Discriminant function analysis was used to classify individuals to each collection site. Two separate analyses were conducted-one using the otolith core data and one using the post-core data. In each case, a stepwise forward selection model, using the Wilk's lambda criterion and an F-test decision criterion of 0.1, was performed to select variables for inclusion in the discriminant function. Four variables (Li, Mg, Cu and Zn) and (Li, Mg, Ni, Cu) were selected from the core and post-core data respectively. Prior to running the discriminant function analysis, a Box's M test was performed to determine if the data met the assumption of equal covariance. Before this test, any samples with missing values in the four variables were omitted; this reduced the core's original dataset from 127 to 108 and the post-core from 127 to 121 samples. In the core dataset, all four variables were missing data. In the post-core dataset, Li was the only variable with a complete dataset. If the assumption of equal covariance was met (p-value > 0.05), a linear discriminant function was performed. If the assumption was violated, a quadratic discriminant function was chosen. A jack-knifed cross-validation was conducted to estimate the proportion of correctly classified samples for each location. To

visualise the trace element differences between the locations, the canonical scores of the first two discriminant functions were plotted for both datasets.

3.3.3 Comparison of core and post-core otolith microchemistry

A mean and standard error plot was created to compare the core and post-core concentrations of each element within each otolith. The plot was also used to visualise the changes in element concentration for the three locations to determine which trace elements showed an ontogenetic or environmental effect. Paired student's t-tests were also performed on each trace element for each capture location. The difference between the positions was calculated for each otolith and was tested for normality and the validity of any outliers was tested using the Grubbs' test. Variables that failed the Grubbs' test were log transformed to bring any outlying variables closer to the mean. If after log transformation, the variable still contained outliers, a Wilcox sign rank test was performed. Because the statistical procedure was conducted for each capture location, the p-value was lowered to 0.017 to account for the multiple comparisons.

3.3.4 Otolith microstructure analysis

Larval otolith microstructure was examined in a subsample of transverse sections that were used in the microchemistry analysis. The primordium of 85 otoliths was viewed using a light microscope (Olympus BX51TF) connected to a digital camera (Q Imaging Retiga 2000R) with a PC interface. To improve clarity, the sections were viewed at a magnification of 2000X with oil immersion. Each primordium was photographed with the Image Pro Analyzer program (Version 6.2) and, using the calliper function within the program, the larval increment widths of the first 12 growth rings were measured and recorded. Multiple readings were taken from 15 otoliths to evaluate precision. Each otolith was counted on three separate occasions by the same reader. The reader counted the larval increments from the hatch line to at least the eleventh growth ring. The final mean coefficient of variation (CV_m) was calculated as

$$CV_m = \frac{1}{15}\sum_{j=1}^{15} CV_j = 100 \times \frac{SD}{Mean}$$

where CV_j is the coefficient of variation for the three readings. The mean increment width per growth ring was calculated and plotted (Figure 3.4). The plot of mean increment

widths revealed some differences between areas at rings 7- 12 which warranted further investigation. The cumulative increment width of rings 7 -12 for each otolith was calculated, checked for normality and equal variance and an analysis of variance was performed to compare mean increment widths between capture locations.

3.4 Results

3.4.1 Otolith microchemical analysis

Core

The quadratic discriminant function separated the samples from the Bay of Biscay, Canada and Venezuela with a classification success of 70%, 15% and 79% respectively (Table 3.3). The canonical discriminant function plot revealed a separation between the Bay of Biscay and Venezuela samples along the first canonical axis (Figure 3.5). There was little separation of the Canadian samples from the other two capture locations along the second axis. These results are also shown in the trace elements standardized canonical coefficients (Table 3.4).

Post-core

The linear discriminant function classified the Bay of Biscay, Canada and Venezuela samples with a success rate of 36%, 26% and 77% respectively (Table 3.5). The canonical discriminant plot showed a high degree of overlap in the elemental concentrations of each group at this life stage (Figure 3.6). Mg made the largest contribution to the first canonical function while the second canonical function was driven mainly by Li, Cu and Ni (Table 3.6).

3.4.2 Comparison of core and post-core otolith microchemistry

The mean and standard error plot showed the trace element concentration differences between core and post-core at each capture location. According to the plot, the change between core and post-core for Venezuela's Mg and Co are different from Canada and Bay of Biscay. These changes; however, were not significantly different (p-value: Mg = 0.07, Co = 0.23). For the Canadian and Bay of Biscay samples, there were no differences in trace element concentrations between the core and post-core. The changes between the two positions for the other elements, for example, Strontium and Barium, were similar for the three locations indicating a consistent ontogenetic effect for all three locations

(Figure 3.7). For both Strontium and Barium, the changes between the spot positions for the three capture locations were significantly different (p-value: Sr = < 0.001, Ba = < 0.01).

3.4.3 Otolith microstructure analysis

The results of the CV test showed that there was a reader error rate of 11.8% on average with a range from 0.8 to 45.7%. There was no significant difference between the three locations in the cumulative width of larval increments 7-12 (ANOVA, p-value = 0.932) (Figure 3.8). Due to the small number of individuals in the sample from Canada, the standard error was large.

3.5 Discussion

The aim of this study was to use otolith trace element concentrations and larval increment widths to determine if albacore caught as juveniles in the Bay of Biscay and as adults offshore of Canada and Venezuela, had shared a common larval and pre-juvenile environment. Differences in larval otolith microchemistry were detected that may reflect the existence of multiple larval populations in the North Atlantic. Trace elemental concentrations at the otolith core were used to discriminate albacore caught as juveniles (ages 1 to 3) in the Bay of Biscay from adult albacore of the same year classes caught off the coast of Venezuela as 6-8-year-olds with a classification success of 70% and 79% respectively. This suggests that there are differences in early life history between the albacore which feed in the Bay of Biscay as juveniles and the albacore that occur off the coast of Venezuela as adults. Those differences may occur due to variation in the internal environment of the fish or the external surroundings in which they live. The trace elemental concentrations of the adult albacore from Canada overlapped with those of the two other groups suggesting that individuals with both types of early life history occur in that area. The results of the otolith microstructure analysis showed no evidence of differences in larval growth between albacore caught in the three areas. This suggests that as larvae the albacore from the three areas encountered similar growing conditions (temperature and food availability) and that the elemental differences were caused by other exogenous factors.

Many studies have examined the role of trace elements in fish's biological processes and their relationship with the ambient environment (Chang and Geffen, 2012; Sturrock et al., 2012). The influence of various endogenous and exogenous factors on otolith composition varies across studies and appears to be species-specific (Stanley et al., 2015). In our study, we observed both ontogenetic and geographic variation in elemental concentrations. Strontium and Barium varied between the core and post-core in all locations but showed no variation within each life stage that might indicate environmental differences in the larval environment. In contrast, concentrations of Magnesium, Lithium, Zinc and Copper at the larval core varied between fish from the three capture locations (suggesting different larval origins) but did not differ between the core and post-core regions of the otolith. This suggests that for this species, these four elements are more influenced by external conditions rather than by ontogenetic development.

Identifying the exact cause of the observed differences in elemental concentrations is difficult and beyond the scope of the current study. Evidence from previous experimental studies can help to identify possible underlying mechanisms but is often contradictory and direct links between concentrations in the environment and those in the otolith are difficult to establish. The incorporation of Magnesium into the otolith has been linked to temperature with studies reporting positive and negative correlations as well as no significant effect. Fowler et al. (1995) found that Magnesium otolith concentration ratios decreased when the temperature was increased while Stanley et al. (2015) found a weak positive relationship between the element and temperature. The reported lack of correlation between Magnesium concentrations in the otolith and those in the water or food suggest that the element is physiologically regulated and may not be a reliable indicator of the availability of the element in the environment (Buckel et al., 2004; Woodcock et al., 2012).

Otolith concentrations of Lithium are higher in saltwater than in freshwater (Hicks *et al.* 2010), due to corresponding changes in Lithium concentrations in the water along a salinity gradient (Milton and Chenery, 2001). While Arai et al. (2007) found a significant relationship between concentrations of Zinc in the otolith and the surrounding water, Ranaldi and Gagnon (2008) found that otolith concentrations of Zinc were correlated with concentrations in the diet but not the water. Milton and Chenery (2001) found a significant correlation between concentrations of Copper in the otolith and the ambient water but not the diet. In short, elemental concentrations reflect the combined influence of the

availability of the element in the water and the diet as well as ambient temperature and salinity overlaid by physiological regulation.

Although differences in core elemental concentrations were evident between the three capture locations, the otolith microstructure analysis showed no difference in larval otolith growth rates. In the microstructure study, the incremental widths of the first 12 growth rings were measured. The mean widths of the first six rings were similar between the three locations. If albacore larvae are still reliant on the yolk sac for nourishment when the first six increments are formed, this could in part explain why larval growth rates were similar across locations during that time period. It is not known when the first increment is formed in North Atlantic albacore tuna and whether this occurs before or after the onset of exogenous feeding. However, evidence from other tuna species suggests that increments are not formed before the yolk sac is absorbed; in bluefin tuna (*Thunnus thynnus)*, increment formation begins approximately four days after hatching which coincides with the start of exogenous feeding (Itoh et al., 2000). Laboratory investigation of increment formation in albacore embryos and early larvae is needed to establish whether the widths of the first six increments reflect external feeding conditions or internal reserves. Interestingly, there were small differences between the three locations in the widths of increments 7 – 12. Although these changes were not found to be significantly different between the capture locations, it would be interesting to investigate whether or not significant differences in otolith growth occur beyond the 12^{th} increment. Another factor to consider is the level of precision associated with the microstructure measurements (mean CV of repeated readings 11%), which could have decreased the sensitivity of the method. Further work on using more discerning statistical methods and expanding the study period could reveal similar differences as those observed in the microchemistry study.

While we can only speculate as to the exact cause of the observed variation in the concentrations of Magnesium, Lithium, Zinc and Copper at the larval core of albacore tuna otoliths, the fact that concentrations differ between fish from different capture locations indicates that these fish are from distinct larval sources. The post-core analysis showed a high degree of overlap in the post-larval elemental concentrations, particularly between Bay of Biscay and Canada. There was also more variability in the elemental concentrations within each group. It was still possible to distinguish fish captured in Venezuela from the other two sites with an accuracy of 77%. The results suggest that as

larvae disperse from the spawning areas, their environments or endogenous conditions become less distinct (with the exception of some of the fish that were collected as adults in Venezuela). Overall, we observe that the three groups are more distinct at the larval stage than at the post-larval stage. This is consistent with the hypothesis that the larvae were spawned in different areas and later dispersed to inhabit a broader range of environmental concentrations.

Currently, albacore in the North Atlantic is managed as one homogenous stock and individuals from different geographical areas are assumed to share similar life history characteristics. Previous studies, using microsatellites (Davies et al., 2011), otolith shape analysis (Duncan et al., 2018), growth differences (Ortiz De Zarate et al., 1996) and otolith microchemistry (Fraile et al., 2016) have indicated that subunits with different life history characteristics may exist in the North Atlantic. The existence of geographic differences in otolith core microchemistry supports this hypothesis. We have shown that albacore caught as adults around Venezuela are not from the same group as juveniles caught in the Bay of Biscay (Figure 3.5). Although there was some overlap in the elemental concentrations, the observed differences between the groups indicate that they are not from a single homogenous larval pool. The results suggest that after wintering in the Central Atlantic, adults migrate to the western Atlantic and spawn in at least two distinct locations. After the first month, pre-juveniles dispersed to areas which share similar environmental characteristics producing more overlap in the otolith elemental concentrations. By using information stored in otoliths to indirectly study the early life stages, this study has provided insight into the first year of life of albacore tuna in the Atlantic.

In 2016, the ICCAT's Standing Committee on Research and Statistics recommended a research programme be initiated to improve the knowledge of biology, ecology, stock status and management of North Atlantic albacore (ICCAT, 2016). Dedicated sampling of spawning adults and larvae, which has not been conducted since 1969 (Richards, 1969; Ueyanagi, 1971), would help to address the uncertainties surrounding stock structure, migration routes and early life history but would require considerable resources. In the absence of such a sampling program, otoliths from juveniles and adults from the commercial fishery can provide information concerning albacore's early life stages as demonstrated in this study. The samples used in this study were obtained through opportunistic sampling. A targeted biological sampling program of the commercial

fisheries could facilitate a more comprehensive investigation of albacore tuna population structure in the North Atlantic. Such a program could also provide material for genetic, stable isotope and otolith microchemistry analyses to support a holistic approach to elucidating stock structure.

In conclusion, otolith microchemistry analysis has shown that there are albacore groups within the North Atlantic stock which display significant differences in otolith core trace element concentrations suggesting distinct larval origins adding to the growing body of evidence of stock complexity.

Table 3. 1 Number of samples obtained for the study separated by Cohort, Capture location and Capture year. Values in brackets represent the number of samples used in the microstructure analysis

		Capture Year									
Location	FL (cm)	2009	2010	2012	2014	2015	2009	2010	2012	2014	2015
		2007 cohort					*2008 cohort*				
Bay of Biscay	68	3 (1)	16 (10)				8 (7)	12 (8)			
Canada	96			3 (2)	3 (1)	1 (1)				6 (5)	3 (3)
Venezuela	100				18 (12)	17 (8)				12 (8)	25 (17)

Table 3. 2 Estimates of precision, accuracy and limits of detection for standards NIST 612 and MACS 3

	NIST 612 SRM				MACS 3			
Element	**Mean Value (ppm)**	**RSD (%)**	**Accuracy (%)**	**Mean LOD**	**Mean Value (ppm)**	**RSD (%)**	**Accuracy (%)**	**Mean LOD**
Li	42.06	1.10	104.62	0.132	62.2	5.61	108.35	0.143
Mg	77.05	0.81	100.1	0.125	1756	5.08	122.06	0.695
Mn	38.02	1.46	98.25	0.106	536	4.57	99.10	0.205
Fe	51.00	1.00	99.99	1.214	11200	5.34	90.11	2.019
Co	35.02	0.75	98.64	0.053	57.1	5.54	93.66	0.063
Ni	37.04	0.91	100	0.084	120	5.34	105.12	0.092
Cu	38.82	1.02	97.98	0.093	57.4	5.61	91.08	0.103
Zn	38.10	1.76	97.44	0.161	111	9.08	100.59	0.144
Sr	78.42	1.00	100	0.656	6760	4.78	91.87	1.672
Ba	39.74	0.94	100.1	0.050	58.7	5.16	109.59	0.065

Table 3. 3 The results of the jack-knife classification of the core data

	Biscay	Canada	Venezuela	Percentage
Biscay	26	3	8	**70.3**
Canada	7	2	4	**15.4**
Venezuela	10	2	46	**79.3**

Table 3. 4 The trace elements standardized canonical coefficients used in the core data analysis

Trace element	Canonical axis 1	Canonical axis 2
Mg	1.47	0.32
Li	-0.39	0.58
Cu	-0.58	0.65
Zn	-0.86	-0.21

Table 3. 5 Results of the jack-knife classification function on the post-core data

	Biscay	Canada	Venezuela	Percentage
Biscay	13	2	21	**36.1**
Canada	4	4	7	**26.7**
Venezuela	14	2	54	**77.1**

Table 3. 6 Standardized canonical coefficients for the trace elements used in the post-core data analysis

Trace element	Canonical axis 1	Canonical axis 2
Li	0.74	0.02
Mg	-1.16	-0.25
Ni	0.01	0.74
Cu	-0.34	-0.68

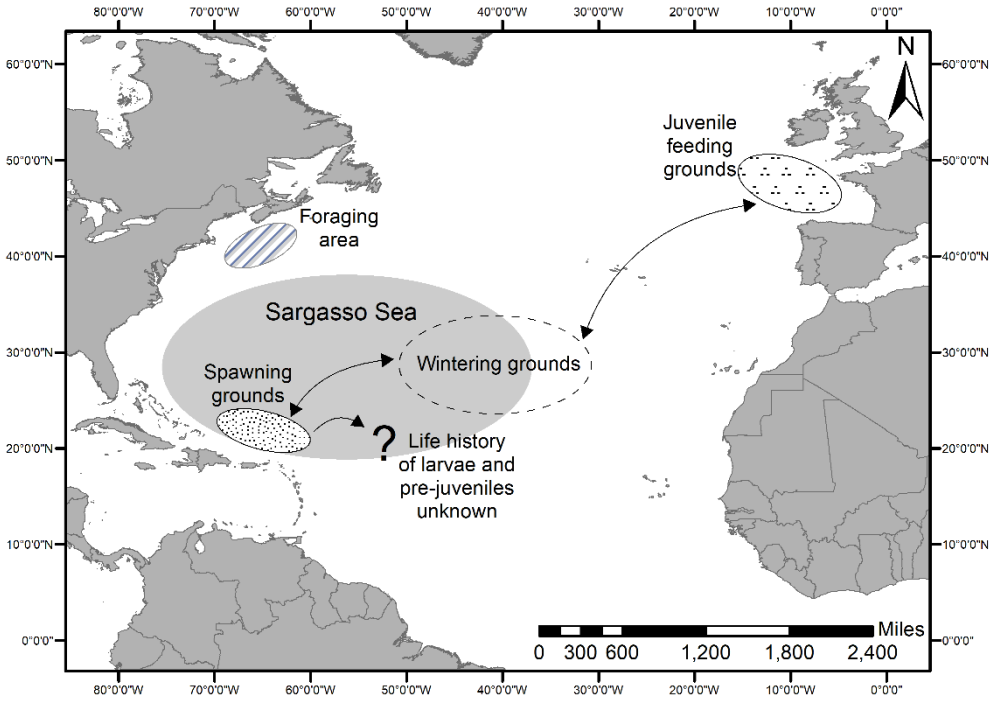

Figure 3. 1 Map displaying putative life-stage specific migration routes of albacore tuna

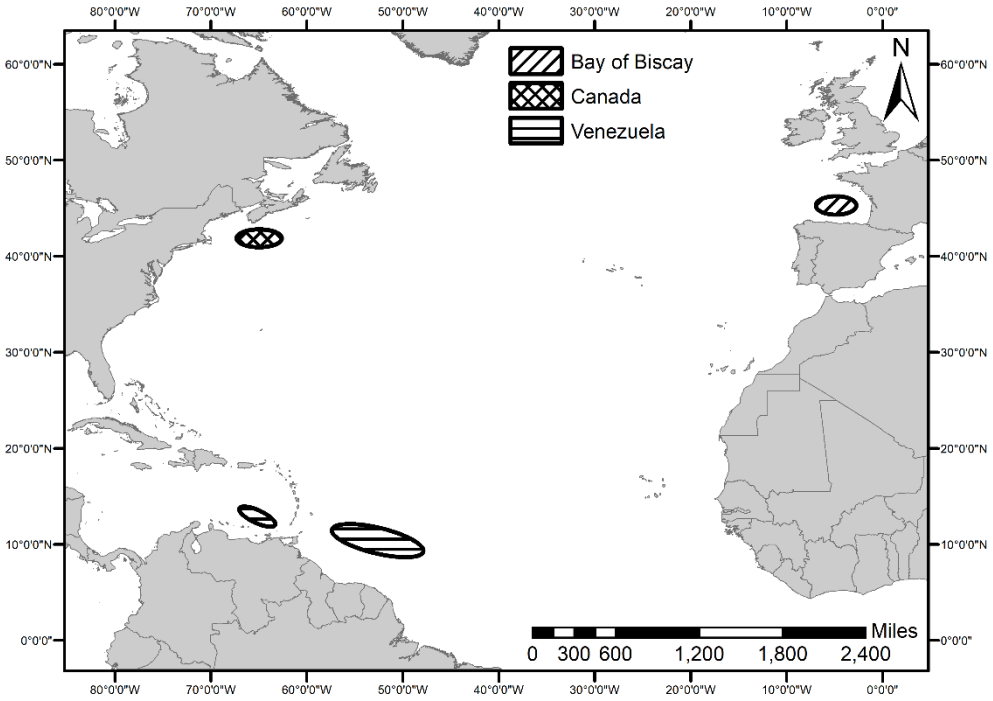

Figure 3. 2 Map of the capture locations of albacore tuna used in this study

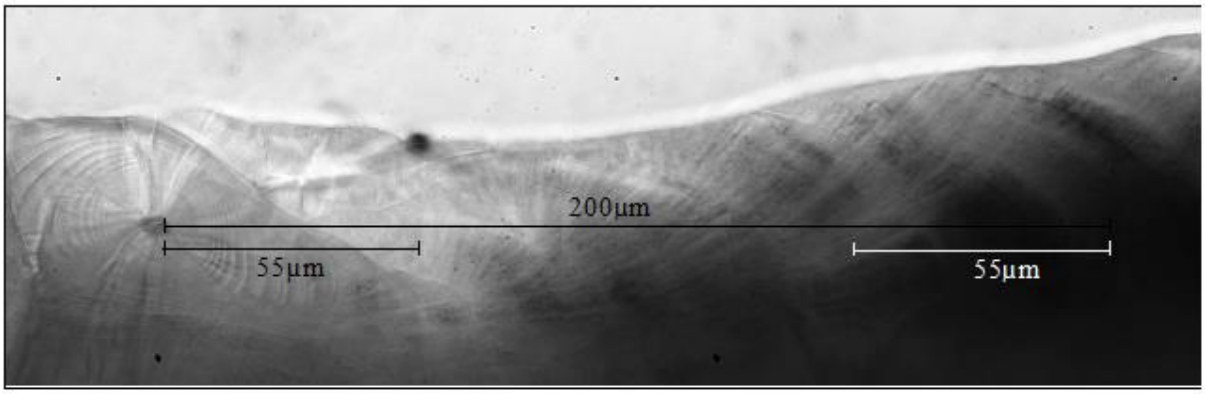

Figure 3. 3 The approximate position of the laser spots. The lines show the distance between the core and the post-core as well as the diameter of the ablation spots which was 55µm.

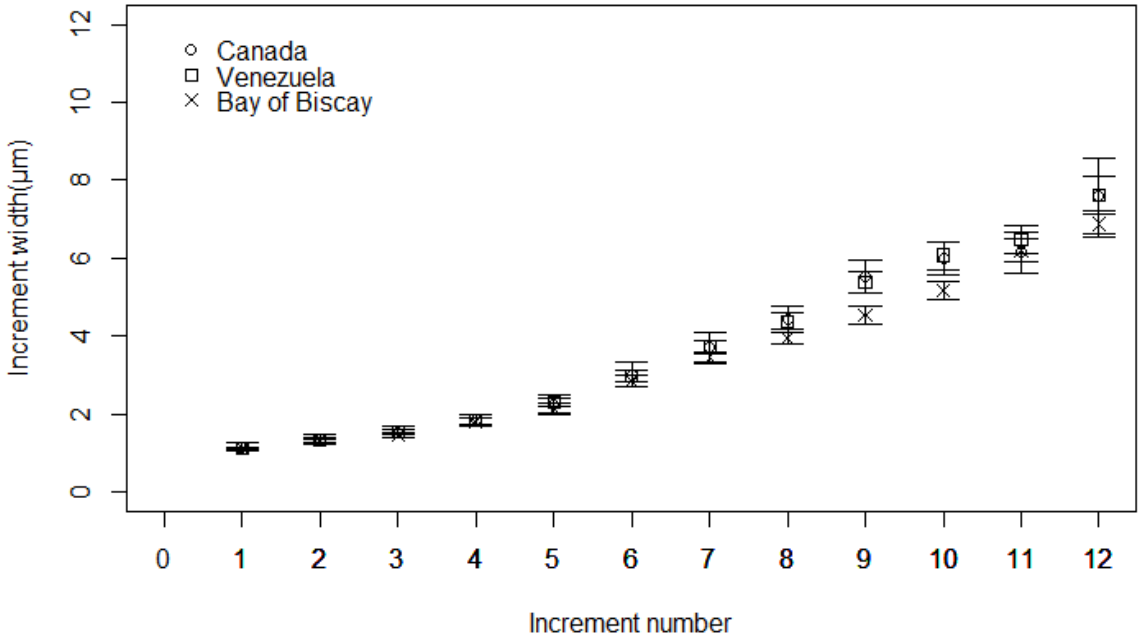

Figure 3. 4 Mean larval increment width per growth ring for each location

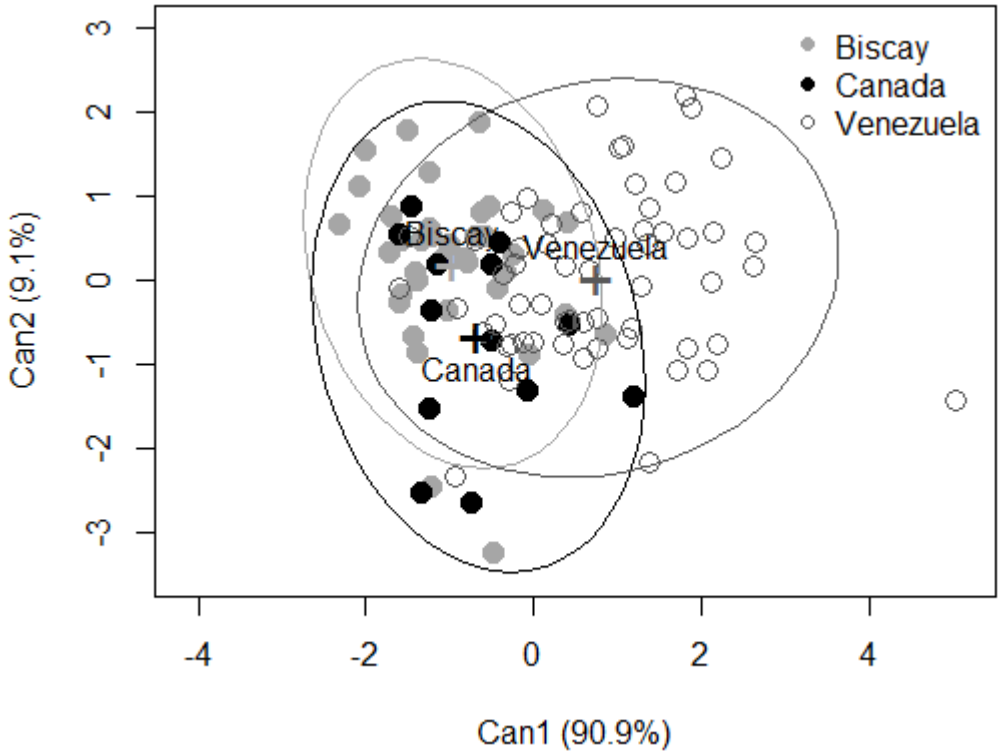

Figure 3. 5 Canonical scores plot using the core natural logged data of samples taken from three capture locations. The ellipses represent 95% confidence levels around the mean for each location.

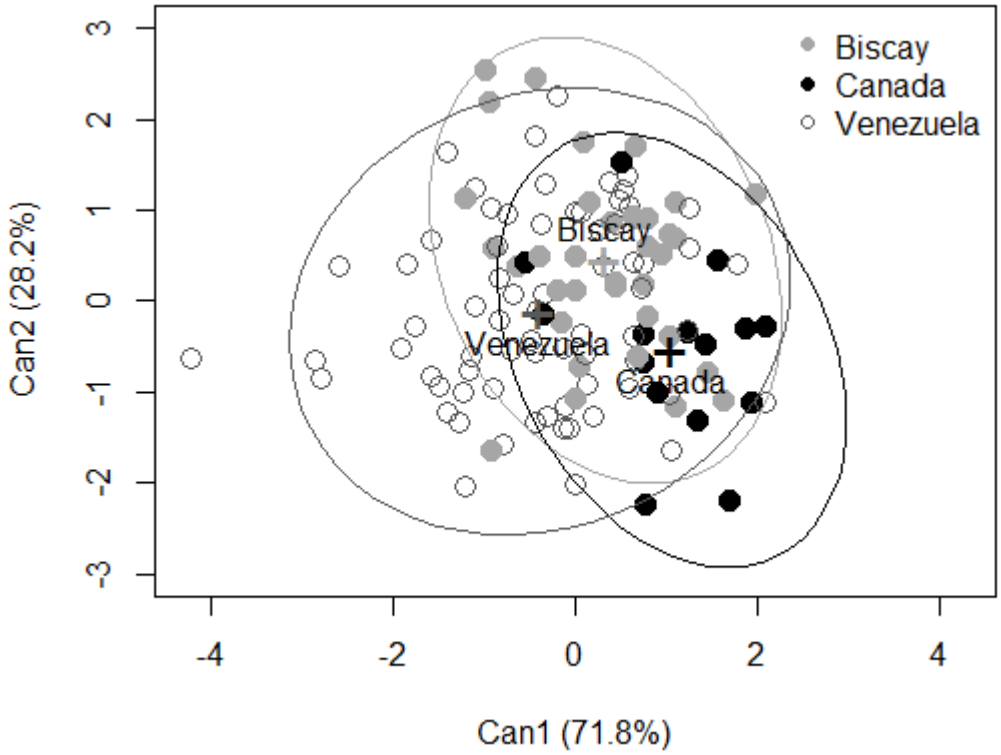

Figure 3. 6 Plot of the canonical scores using post-core natural logged data of samples taken from three capture locations. The ellipses represent 95% confidence levels around the mean for each location.

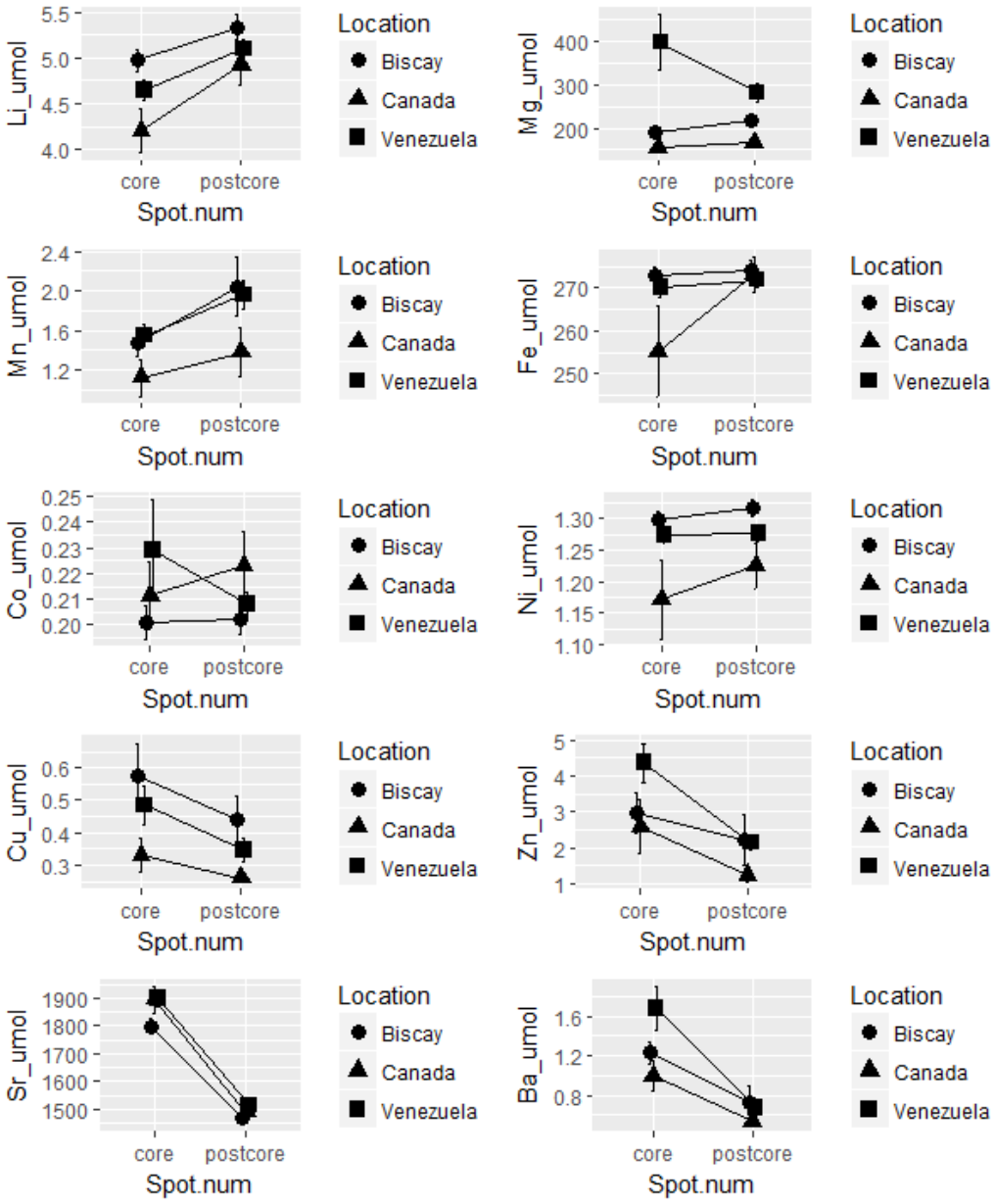

Figure 3. 7 Plot of the mean and standard error for each trace element for each capture location

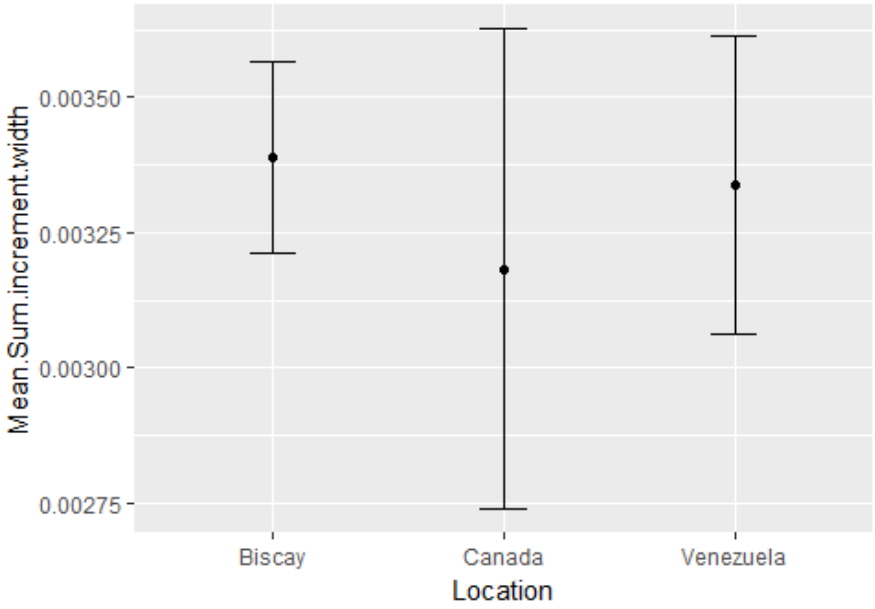

Figure 3. 8 Plot of the mean sum of the increment widths of larval growth rings 7-12 for the three capture locations

Chapter 4: Hidden semi-Markov modelling of vessel monitoring system (VMS) data accurately quantifies fishing activity and improves catch standardisation for albacore tuna (*Thunnus alalunga)*

4.1 Abstract

The use of fishery-dependent sources to derive indices of abundance relies on the assumption that catchability is constant; however, the behaviour of the fishing fleet can affect the catchability of the species. Vessel monitoring systems (VMS) capture high resolution data describing spatial and temporal variability in fleet behaviour which can inform the interpretation of catch-effort data. This study uses VMS and observer data from the Irish mid-water pair trawl fishery in the North-east Atlantic to identify pairs of vessels which operate as a fishing unit and to quantify fishing effort. Hidden semi-Markov models (HSMMs) distinguished between fishing and non-fishing activity with an accuracy of 87%. CPUE standardisation models were improved by combining catches across vessel pairs and by including model-derived estimates of fishing effort instead of days at sea. Low and high components in the catch data were explained by the unequal sharing of catches between paired vessels. The results show that using VMS data to describe fleet behaviour can improve catch rate standardisation for albacore tuna.

4.2 Introduction

Stock assessments are used to evaluate the status of a stock in relation to reference points, appropriate for the proper management of the target species (Hare and Richardson, 2013; Hilborn and Walters, 1992). The input to a stock assessment depends on the data available and the type of model being used. Generally, estimates of natural mortality and relative abundance are required (Maunder and Punt, 2004). Such data are often obtained from fishery dependent sources due to the prohibitive costs of dedicated scientific surveys, especially for highly migratory species, such as tunas (Cosgrove et al., 2014c; Maunder et al., 2006). The use of catch per unit effort (CPUE) from the commercial fishery as an index of abundance assumes that CPUE is proportional to the abundance of the stock. The caveat to this assumption is that catchability is not always constant (Maunder et al., 2006). Changes in the distribution of the population and the behaviour of the fishing fleet can affect the catchability of a target stock; particularly in shoaling species. As abundance decreases, a decrease in catch may be observed, but the proportional catchability may increase, especially if there is no change in the size of the shoals (Maunder et al., 2006). Misinterpretation of high CPUE estimates can lead to overestimated stock size, inflated quotas, untenable fishing pressure and the subsequent overfishing of the stock (Rose and

Kulka, 1999). One way to prevent this is to standardize CPUE estimates to account for changes in catch rate that are not related to changes in abundance.

Modelling of fleet behaviour can improve estimates of the pressure that is exercised by fishing vessels (Vermard et al., 2010) and could help to develop appropriate catch-effort standardizations. Hidden Markov (HMMs) and hidden semi-Markov models (HSMMs) can be used to spatially and temporally characterise fishing trips and to discriminate between different types of behaviours (e.g. fishing and steaming) (Vermard et al., 2010; Walker and Bez, 2010). These models use in situ observed data, for example, step lengths, vessel speed and turning angles, to predict via probabilistic inference, the behavioural states of the vessel during the trip. Joo et al. (2013) used HSMMs to characterise the movement of Peruvian anchovy purse-seiners into states of cruising, searching and fishing using data from Vessel Monitoring Systems and from on-board observers, demonstrating the application of the modelling approach to this type of movement data.

Satellite-based Vessel Monitoring Systems (VMS) were introduced in 1998 by the European Commission (EC) with the objective of monitoring European fishing vessels for security control and enforcement functions (European Commission, 1997). Since 2005, it has been mandatory for all vessels over a length of 15 m to transmit their position and information regarding their speed, course or heading at two-hour intervals, or less (European Commission, 2003). This creates a data set of fine-scale spatial and temporal vessel movement data which may be used to better understand the behaviour of vessels at sea. VMS records do not indicate the activity of a vessel, therefore, insight into their activities is provided by on-board observers. Although, it is not economically feasible to get observer data from every vessel within a fleet, models which are able to predict the activity of the vessels can be used to improve the measure of effort used in the estimation of CPUE.

Albacore tuna, (*Thunnus alalunga*) is a highly migratory temperate species and is one of the most economically important tuna species globally. In the Atlantic Ocean, albacore tuna is separated into three stocks for management purposes: North, South and Mediterranean. Within the North Atlantic, albacore tuna is exploited by longline and surface fisheries (Cosgrove et al., 2014a; ICCAT, 2016; Lehodey et al., 2014). The longline fleet consists of mainly Chinese-Taiwanese, Japanese and South Korean fishing vessels that target sub-adult and adult (60-130 cm fork length) albacore all year-round in

the central and western regions of North Atlantic (5°N - 35°N, 30°W - 75°W) (ICCAT, 2016; Lehodey et al., 2014). Surface fishing vessels, composed of baitboat, trolls and mid-water pair trawls from France, Ireland, Spain and Portugal target immature (50-90 cm FL) albacore during their feeding migration (June-October) to the productive waters around the Azores and Canary Islands, in the Bay of Biscay and to the southwest of Ireland (Dufour et al., 2010; ICCAT, 2011). From 2012-2015, the highest catches of Atlantic albacore were in the North-east Atlantic with surface fisheries making up 80% of the northern catch (ICCAT, 2016).

The Irish mid-water pair trawl (MWPT) fishery commenced fishing for albacore tuna in 1998 and it accounts for approximately 15% of the surface fishery(Cosgrove et al., 2014b; ICCAT, 2016). Albacore is one of the country's top-value species for export, largely to Spain and France and is a commodity worth approximately 17 million euros (Bord Iascaigh Mhara, 2016). Presently, Irish catch and effort time series data are not used in ICCAT albacore stock assessments because the data contains large inter-annual variabilities, creating highly variable standardised abundance indices, which if used, could result in unreliable stock assessments (Cosgrove et al., 2014c). Using finite mixture models, Cosgrove et al. (2014c) identified two components in the catches; it was hypothesised that the low catch component represented trips where the majority of the time at sea was spent searching for the shoal, while the high catch component represented trips where the shoals were located and the majority of the trip was spent fishing. The authors also suggested that HSMMs and VMS data could be used to test this hypothesis and could potentially improve the Irish standardised CPUE indices. Therefore, the aim of this study was to investigate the influence of fleet behaviour on catch per unit effort estimates by analysing observer and VMS-logbook data from the Irish mid-water pair trawl fishery using hidden semi-Markov models. The potential to improve CPUE standardisation by incorporating VMS-based estimates of fishing activity was also examined using finite mixture models.

4.3 Methods and Materials

4.3.1 Markovian models

Markovian models have been applied in various fields, for example, speech recognition, MRI brain mapping, econometrics and animal movement (Langrock et al., 2012; Peel et

al., 2011; Yu, 2010). They require information on the number of states to be determined in the data, the probability of being in a behavioural state at the beginning of a trip (initial distribution), the probability of transiting from one state to another (transmission distribution) and the conditional distributions of the observation data for each state in the model (emission distribution). The models use an expectation-maximization (EM) algorithm to estimate the distribution parameters of the states and to assign trip data to each state (Natale et al., 2015). The distinction between HMMs and HSMMs lies in the distribution of duration time, the amount of time spent in a given state. Duration time in HMMs follows a geometric distribution. In some real-life situations, the transition from one state to another depends on the amount of time spent in the current state, therefore, a geometric distribution is not realistic (Joo et al., 2013; O'Connell and Højsgaard, 2011; van de Kerk et al., 2015). HSMMs are able to characterise state transition over the period of time spent in a specific state which is key when modelling fishing vessel behaviour.

4.3.2 Data collection

On-board observer and VMS data from the Irish MWPT fishery were obtained from the Irish Marine Institute. The observer data consisted of the day, month, geographic position, vessel speed and course, haul number and activity type for thirteen trips. To preserve anonymity, the year of each trip and names of the vessels were removed from the dataset. The VMS data, with corresponding logbook information, contained information pertaining to trips where at least 80% of the landings were reported as albacore from 2006 to 2016. Also, to anonymise the actual tracks of the vessels, the positional information in the VMS data were transformed so they did not relate to a known position but the distance between individual points remained unchanged.

4.3.3 Observer data

The types of activity included in the observer data were steaming, searching, shooting the net, fishing, hauling the net, knocked out (engine is off) and dodging (avoiding inclement weather). Since shooting and hauling the net was an active process, it was considered a part of the overall fishing event (Graham Johnston, personal communication, June 8, 2017). The time periods of remaining activities (steaming, searching, knocked out and dodging) were not recorded, therefore they were pooled together and considered as non-fishing phases. The observer data were split into two, a training dataset (eight trips) and

a testing (five trips) dataset. The states to be determined in the test data were Fishing and Non-fishing. Prior to analysis, records with a speed of zero or missing speed values were omitted from both datasets.

Using the training data, the mean speed and variance were calculated for the fishing events and the non-fishing phases for the emission distribution. The duration of each fishing event was calculated by summing the time it took to complete a fishing event, from shooting to hauling in the net. The observer data did not contain sufficient information to calculate the duration of each non-fishing phase, therefore, a uniform distribution was assumed, and the minimum and maximum duration recorded across all non-fishing phases were used to estimate an appropriate range of values. After the removal of missing and zero speed records, the test data consisted of 151 records for five trips. Using the initial, transmission, emission and duration distributions, the starting values for the model were generated using the hsmmspec function from the mhsmm package in R (Version 0.4.16). Using the speed values from the test dataset and the generated starting values, the parameters of the HSMM was created using the EM algorithm. The predicted state of each test data record was stored and cross-validated with the test data's recorded activity. Model indicators of accuracy, recall, precision and F-measure were calculated to evaluate the model's performance (Table 4.1).

4.3.4 VMS data

The data were cleaned to remove discrepancies arising from minor changes (1-6 minute) in the time interval, inaccurate port entry and exit records, time gaps in vessel records, erroneous time entries, vessels and individual trips with no consistent time interval, trips with no clear beginning or end and changes in the time interval during a trip. Once cleaned, the data was separated by year and each individual trip for each vessel was labelled with an ID number (Vessel number_trip number). Altogether, the data comprised of 561 trips from 51vessels with over 56,000 records. Each record consisted of the ID number for each trip, a 2-hour timestamp, the vessel speed, a "Port" or "At Sea" label, and the catch of the trip. All entries labelled as "Port" were removed from each dataset and the vessel speed values, along with the starting values from the observer training dataset were included in the HSMM.

For each year, a table was created to include the start and end date, the length of each trip in hours, the catch, the CPUE estimate (the quotient of catch and trip time), the predicted fishing hours (number of hours of fishing activity predicted by the HSMM), the estimated catch per unit effort in hours of fishing (CPUF) (the quotient of catch divided by number of hours fishing estimated by the HSMM) and the fishing proportion (the quotient of fishing hours divided by total trip time). The correlation between the CPUE estimate and the fishing proportion was calculated for each year to determine if CPUE estimates were influenced by fleet behaviour. If CPUE was influenced by the proportion of time spent fishing, positive and strong correlations were expected. The majority of the correlations were found to be weak and negative with non-significant p-values (two years had a p-value < 0.05; however, the correlation was negative). It was also noted that some trips, for which very low catches were reported, had a high proportion of fishing activity (part of the low catch component identified by Cosgrove et al. (2014c). At this point, the approach of the study was reviewed.

The second phase of the analysis involved the identification of paired vessels. Mid-water pair trawls operate in the open ocean's midwater layers and require two boats to tow the net (Vijayan, 2009). During the trip, either boat can shoot and haul in the net (FAO, 2001), therefore the total catch from the trip is divided, often unequally, between the two vessels and is reported in the logbooks as separate catches. To identify fishing pairs in each year, trips with similar start and end dates were grouped and plotted together to determine which trips had similar tracks. If both the shape of the tracks and the trip duration were similar, the two boats were considered a working pair and their catches were summed.

Data for the fishing pairs (180 pairs), were separated by year and the HSMM model was rerun. Each year table was recalculated to include the paired data and two additional columns: the steaming time (in hours) to and from the fishing grounds (estimated from the plot of each individual trip) and the hours on the fishing grounds (difference between the trip duration and the steaming time). Therefore, for each trip, the table included the start and end date, the duration of each trip, the steaming time, the hours on fishing grounds, the catch, the CPUE estimate (using hours on fishing grounds as the effort), the predicted fishing hours from the HSMM, the estimated catch per unit effort in hours of fishing (CPUF) and the fishing proportion (the quotient of fishing hours and the hours on fishing grounds). The correlation between CPUE and fishing proportion was tested using the Pearson's correlation coefficient.

4.3.5 Finite mixture models

The finite mixture models developed by Cosgrove et al. (2014c) to standardise CPUE estimates while accounting for multiple components in the catch data were fitted to the fishing pair data using the R package, flexmix (Version 2.3-14). The full methodology is described in Cosgrove et al. (2014c). Positive catches were modelled as a function of effort, year and quarter in a base-case single component lognormal model as shown below (information on fishing zone and vessel size category were not available due to data anonymity restrictions). Three different scenarios were modelled using paired and unpaired data with different methods of quantifying effort: total duration of each trip (in hours) and time spent fishing (as estimated by the HSMM).

Unpaired total effort (UTE)

$$\ln(Unpaired\ Catch) = \ln\ (Trip\ duration\ hours) + Year + Quarter$$

Paired total effort (PTE)

$$\ln(Paired\ Catch) = \ln\ (Trip\ duration\ hours) + Year + Quarter$$

Paired fishing effort (PFE)

$$\ln\ (Paired\ Catch) = \ln\ (Fishing\ hours) + Year + Quarter$$

The finite mixture models allowed for the modelling of the mixture of distributions underlying the catch data in the three scenarios. For each scenario, the most likely number of distributions was determined using all the covariates and the finite mixture model that assumed between 1 – 4 components was compared using the Bayesian Information Criterion (BIC). After the best fitting number of components was determined, the effect of the covariates was investigated using log-likelihood ratio tests (based on 20 model iterations). The UTE model represents the two-component model developed by Cosgrove et al. (2014c). This was compared to the PFE model in terms of normality, skewness and deviance residuals. A generalised linear model was used to calculate the standardised indices for the two models.

4.4 Results

4.4.1 Observer data

The performance indicators for the HSMM showed that the model was able to identify the two behaviour states efficiently, with an accuracy of 86.7%. The values for the other indicators of model performance for both behaviour modes can be found in Table 4.2. The majority of the misclassified fishing events were records of weather dodging and engine knock out. Only one fishing event was misclassified as a non-fishing phase. Also, two net shooting records were misclassified as non-fishing; however, the speeds of the records were not within the fishing speed range.

4.4.2 VMS data

For the paired fishing data, the correlations between fishing proportion and CPUE ranged from -0.33 to 0.58. Although a strong correlation was detected in 2008 the available sample size was small, and the relationship was not significant. Significant correlations were detected in 2011 and 2013 (Table 4.3). The positive correlations suggested that in some years low catch rates were associated with trips which involved a relatively high proportion of searching activity. However, the absence of any correlation in other years indicates that other factors such as seasonal changes in distribution, abundance or fish behaviour are driving most of the variability in catch rates.

4.4.3 Finite Mixture model analysis

For both the PFE and the PTE models the one-component model had the lowest BIC score (Figure 4.1), whereas the best fitting UTE model had two components (as previously observed by Cosgrove et al 2014c). The log-likelihood ratio tests showed that including year and quarter as covariates in the PFE and PTE models improved the model fit (test statistic 17.05 and 16.39 respectively, df = 2, p-value < 0.001). For the UTE model, only year significantly improved the model (test statistic = 3.7, df = 4, p-value with quarter = 0.45).

Comparison of BIC values between the PFE and PTE models showed that expressing effort as time spent fishing instead of total trip duration improved the model fit (Figure 4.1). Even though pairing the vessel data reduced the sample size, a clear reduction was

observed in the variability of the catch data except for the year 2010 (Figure 4.2). The deviance residual histogram and quantile-quantile (Q-Q) plot of the PFE (one-component) and UTE (two-component) models showed that the two shared similar characteristics (Figure 4.3). The PFE model conformed to a normal distribution (Anderson Darling test, A = 0.641 p-value = 0.093) and even though its residuals had a slight negative skew, it was not found to be significant (skewness = -0.346, D'Agostino test, p-value = 0.055). The standardised index plot showed that the PFE model exhibited similar temporal trends as the second component of the UTE model. The trend in the catches from the PFE model appeared stable throughout the time series except in the year 2010 (Figure 4.4). This confirmed that the multiple components that were previously observed in the CPUE data by Cosgrove et al (2014c) could be largely explained by the unequal sharing of catches across paired vessels, with the exception perhaps of 2010.

4.5 Discussion

The aim of this study was to investigate the influence of vessel behaviour on CPUE estimates using data from the Irish mid-water pair trawl fishery. When applied to observer data, the HSMM model was able to differentiate fishing events from non-fishing phases with a high degree of accuracy (86.7%). When this model was used to categorise VMS records as fishing and non-fishing activity, it was found that the relative amount of time spent fishing was not strongly correlated with CPUE in most years, indicating that other factors were driving most of the variability in catch rates. Nonetheless, using fishing activity instead of total trip duration to quantify effort reduce the variability in the CPUE standardization model. The finite mixture analysis showed that the two components previously observed in the CPUE data by Cosgrove et al. (2014c) can be explained by the unequal sharing of catches between paired vessels and can be addressed by considering a vessel pair as the fishing unit. Therefore, using VMS data to identify fishing pairs and to quantify actual fishing effort can reduce the variability in CPUE standardisation.

The analysis of the observer data confirmed that the HSMM was efficient at distinguishing between fishing and non-fishing activity (Table 4.2). The accuracy of the model was similar to that achieved in previous studies. For example, Chang and Yuan (2014) used classification and regression tree analysis of observer and VMS data from the Taiwanese longline fleet in the Pacific Ocean to distinguish fishing and non-fishing activity with an average recall of 89.5% and a mean accuracy of 85.5%. Bertrand et al.

(2008) achieved an 83% success rate when using an artificial neural network model to identify fishing sets in VMS data from Peruvian anchovy purse-seiners. In the present study, misclassification of observer records largely reflected the model's inability to differentiate activities such as dodging inclement weather from fishing events. The model also misclassified some searching entries as fishing, probably because the speed of these activities overlapped with the fishing speed distribution. Also, these misclassifications occurred either right before or between genuine fishing events which might have made it difficult for the model to correctly identify them. This type of misclassification was also observed by Gerritsen and Lordan, (2011) when they used VMS data to model the fishing activity of vessels targeting monkfish in the west of Ireland.

To improve the accuracy of the HSMM, other in-situ variables such as turning angles and step lengths could be included in the analysis. In previous studies, turning angles have been used to distinguish vessel behaviour modes. For example, Walker and Bez, (2010), used both speed and turning angles to characterise vessel behaviour of purse seiners targeting tropical tuna in the Indian Ocean. Joo et al. (2013) also used speed and turning angle, among other variables, in their analyses. However, if vessel speed is the only variable available for use in the model, it can be used to efficiently distinguish fishing events from non-fishing phases.

The lack of any correlation between fishing proportion and CPUE in most years indicates high within-year variability in catch rates, possibly due to seasonal and spatial fluctuations in fish abundance or shoal density. Variability in the abundance and distribution of albacore has been linked to changes in oceanic parameters and food availability. Goñi et al. (2015) observed that albacore tuna preferred to feed and reside in cool waters with high plankton concentrations and found that the vertical distribution of the shoals increased with the depth of the mixed layer. Lezama-Ochoa et al. (2010) also suggested that the availability of anchovy, a primary prey item for albacore, could be altered by changes in sea surface temperature, thus affecting albacore CPUE estimates. Changes in these conditions, both short- and long-term, could alter the vertical and horizontal distribution and the concentration of the stock thereby affecting the catch rates of vessels targeting albacore tuna.

The multiple components in the CPUE data, which were previously reported by Cosgrove et al. (2014c), were no longer detectable when catches from paired vessels were summed

prior to analysis. The standardised index plot showed that the second component, which represented small catches in the data were, in effect, catches taken by one side of the fishing pair (Figure 4.4). This highlights the importance of identifying fishing pairs when estimating the catch per unit effort for mid-water trawl data. The plots of paired catches by year (Figure 4.2) and the standardised CPUE indices (Figure 4.4) showed little variability in the catch rates except in 2010. The high degree of variability and low CPUE index observed for this year was driven by eight very small catches, the majority of which occurred in August. The low CPUE index in 2010 might be a result of catch misreporting or may reflect a real change in the distribution or abundance of the shoals. Fishermen targeting albacore reported a reduction in catches in 2010 compared to previous years as well as a change in the spatial distribution of the schools (McCarthy et al., 2011). The discrepancy does warrant further investigation especially since this decrease in CPUE was also evident in other surface fisheries in the region (Figure 4.5).

The issues identified in the distribution of residuals of the single component model by Cosgrove et al. (2014c) were satisfied by applying a two-component finite mixture model. In this study, these issues can also be addressed by treating vessel pairs as a unit of measurement for calculating effort and CPUE. With the reason for the large interannual variability explained, the paired fishing standardised indices appeared stable over the eleven-year time series except for the year 2010.

Incorporating the HSMM estimates of actual fishing effort in place of total effort succeeded in reducing the variability in the standardisation of the CPUE estimates. The best fitting model (lowest BIC value) explaining variability in albacore catches included predicted fishing time from the HSMM, along with year and quarter (PFE) (Figure 4.1). The model could be further improved by including other relevant variables such as vessel size which was found to be significant in the Cosgrove et al. (2014c) study but was not included in our study due to anonymity restrictions. CPUE is influenced by many variables, for example, fish abundance, spatial and temporal distribution of vessels and gear type. This study; however, demonstrated that vessel behaviour, in terms of time spent fishing, is an important variable that should be included in the catch-effort standardisation process. One precaution to using fishing effort in CPUE standardisation is the increased possibility of hyperstabilising the CPUE estimate (Erisman et al., 2011). Relying on catch data and fishing effort may mask decreases in population abundance, especially for shoaling species where the density of the shoal may stay the same, but the distribution of

the population has decreased. In such situations, VMS data could also be used to monitor changes in fishing proportion over time to alert fisheries management to signs of hyperstability in the CPUE estimates.

The task of identifying fishing pairs was labour intensive because the information on pairs was simply not recorded by management agencies. In a bycatch observer study carried out in 2011-2012, the fishing pairs of pelagic trawling vessels were recorded as they fished for albacore and mackerel, but such recordings are not a customary practice in the management of the fishery (Boyd et al., 2012). Agencies conducting observer trips and reporting albacore landings at ports should begin recording which vessels were partnered for individual trips since this information has been shown to be important for CPUE standardisation. For past datasets where this information was not recorded, one way to reduce the time required to identify fishing pairs, and possibly avoid reductions in sample size due to difficulties associated with manually identifying pairs, is the use of programs, such as VMSbase and VMStools, to visualize fishing vessels using VMS data (Hintzen et al., 2012; Russo et al., 2014). The use of these programs was not possible in this study because the geographic positions of the vessels were transformed to protect the identity and fishing patterns of the vessels.

The classification of fishing activity inferred from the hidden semi-Markov model could be improved with the use of more detailed observer data. In the study, we used a uniform distribution for the non-fishing phases of the data because only the fishing events were closely monitored. To get a better idea of non-fishing duration, fishing trips should be fully monitored; however, it may not be financially feasible to increase the number of observers on vessels. The use of video cameras on board might be a possible tool to assist in the monitoring of fishing vessels (Joo et al., 2013). With the improved detail of fully monitored observer trips, especially in the duration of non-fishing phases, the number of states examined by the model could be increased. This might enhance the model's efficiency in identifying the fishing proportion of trips, for example, the separation of non-fishing activities such as dodging and searching.

In conclusion, the results show that hidden semi-Markov models have the ability to efficiently distinguish behavioural modes from fisheries observer data. Using VMS data, the correlation between fishing proportion and CPUE was not positive and significant for every year which indicates that there is a lot of variability present in the catch data.

Nonetheless, the results show that incorporating vessel behaviour into catch rate standardisation models can reduce the variability in CPUE estimation which is crucial for the proper management and sustainable use of this important species.

Table 4. 1 The calculations used for the indicators of model performance

Accuracy	$\frac{Events\ (phases) correctly\ inferred}{Total} \times 100$
Precision	$\frac{Events (phases) corectly\ inferred}{Sum\ of\ events\ (phases)\ inferred\ by\ model} \times 100$
Recall	$\frac{Events\ (phases) correctly\ inferred}{Sum\ of\ real\ events\ (phases)} \times 100$
F-measure	$\frac{2 \times Precision\ \times Recall}{Precision\ + Recall} \times 100$

Table 4. 2 The performance of the HSMM on the observer data

Accuracy	86.7 %	
	Non-fishing	Fishing
Precision	91.6%	80.8%
Recall	85.4%	88.7%
F-measure	88.3%	84.5%

Table 4. 3 The correlation value of CPUE and fishing proportion for each year with significant correlations in bold

Year	Number of paired trips	Correlation	p-value
2006	4	0.30	0.69
2007	5	0.39	0.52
2008	7	0.65	0.12
2009	22	0.04	0.85
2010	26	0.33	0.10
2011	21	0.48	**0.03**
2012	30	0.20	0.30
2013	13	0.58	**0.04**
2014	18	0.10	0.68
2015	23	0.06	0.79
2016	11	-0.33	0.32

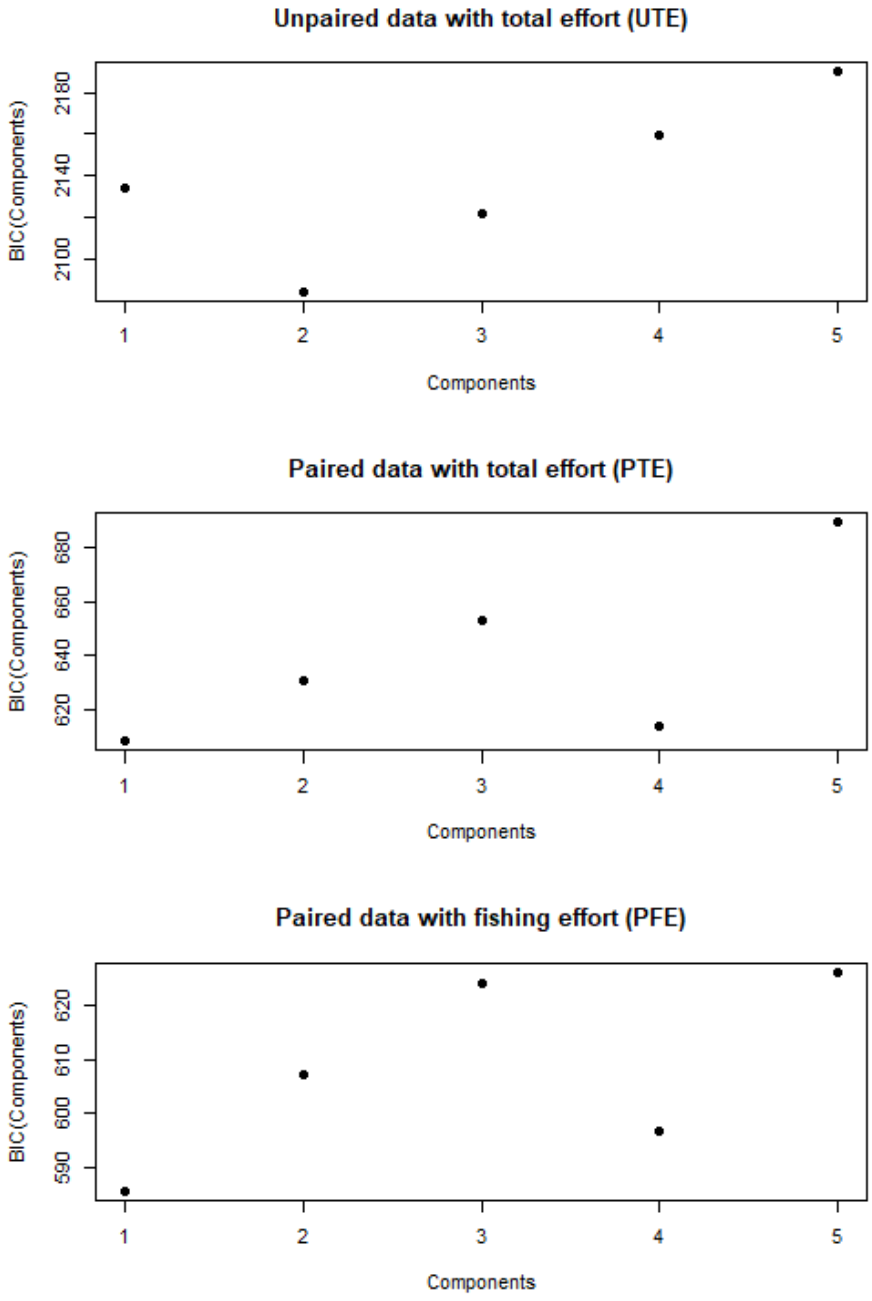

Figure 4. 1 Plot of the Bayesian Information Criterion (BIC) for the three scenario models

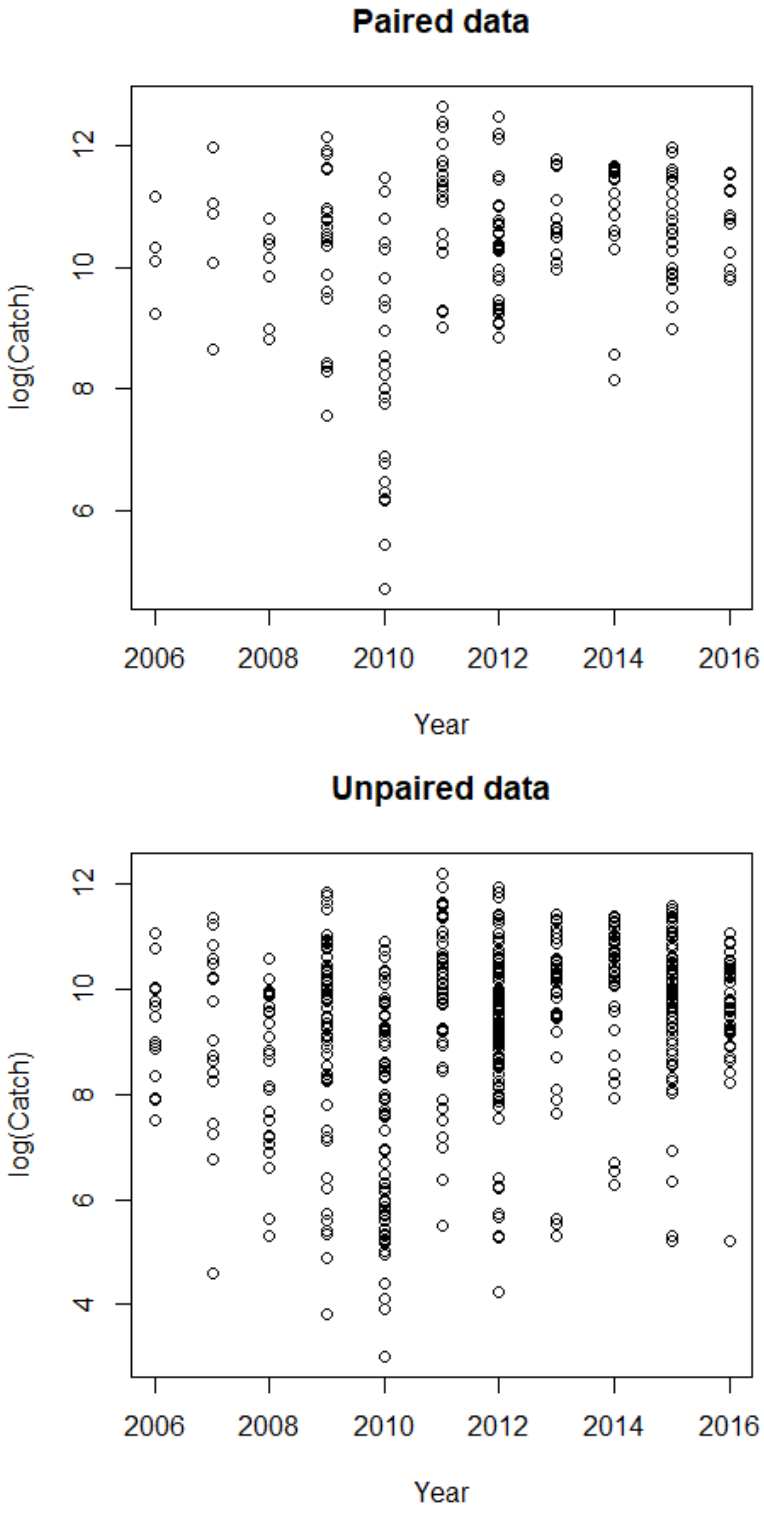

Figure 4. 2 The natural logged catch by year for the paired and unpaired data. For the paired data, each point represents the combined catch of a pair.

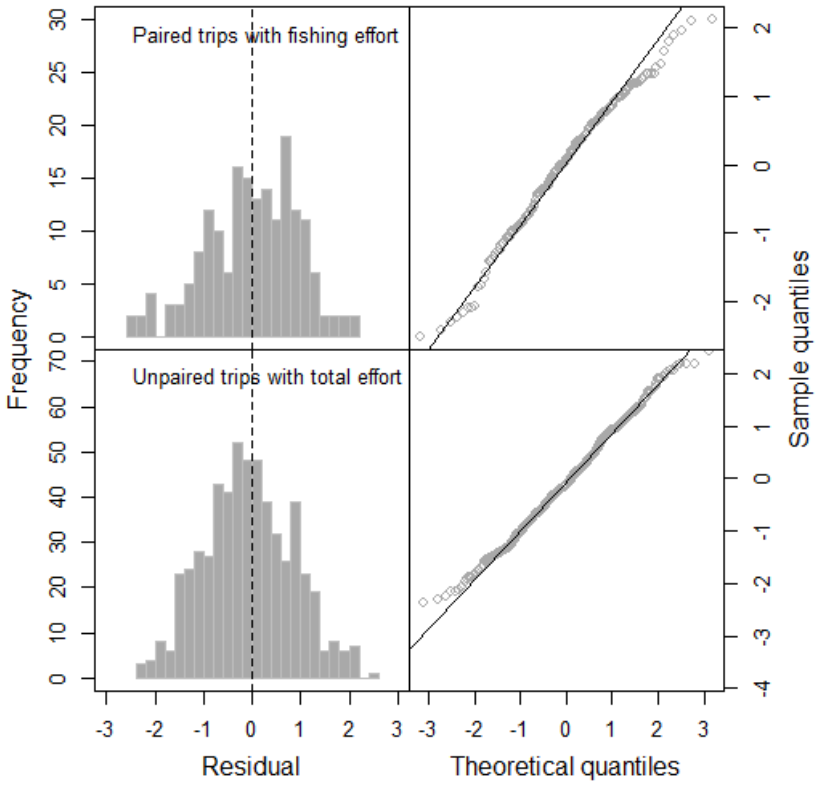

Figure 4. 3 Deviance residual histograms and Q-Q plots of the PFE one-component (top row) and the UTE two-component (bottom row) models.

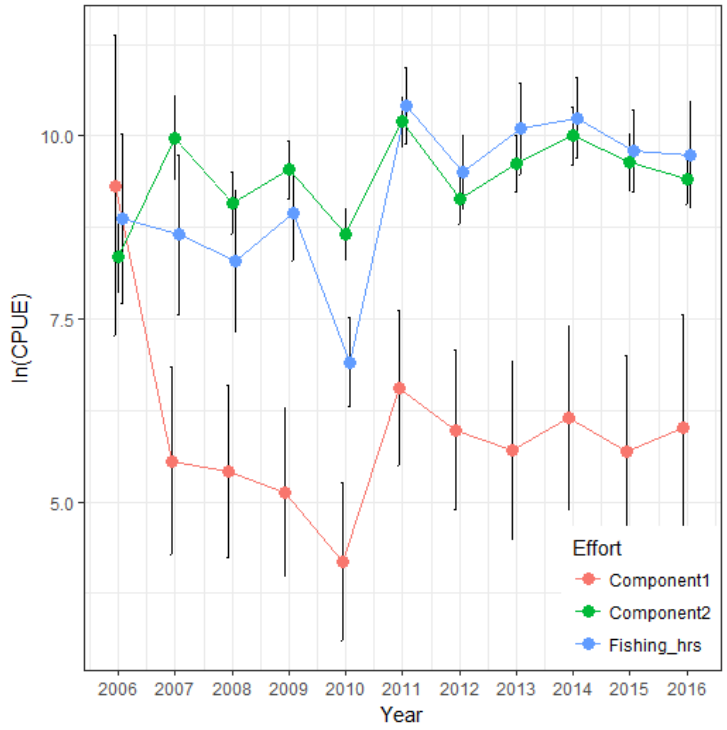

Figure 4. 4 The standardised CPUE indices predicted from the PFE (blue) and the UTE models (component 1: orange, component 2: green. The error bars represent the with 95% confidence intervals for each indice in the time period.

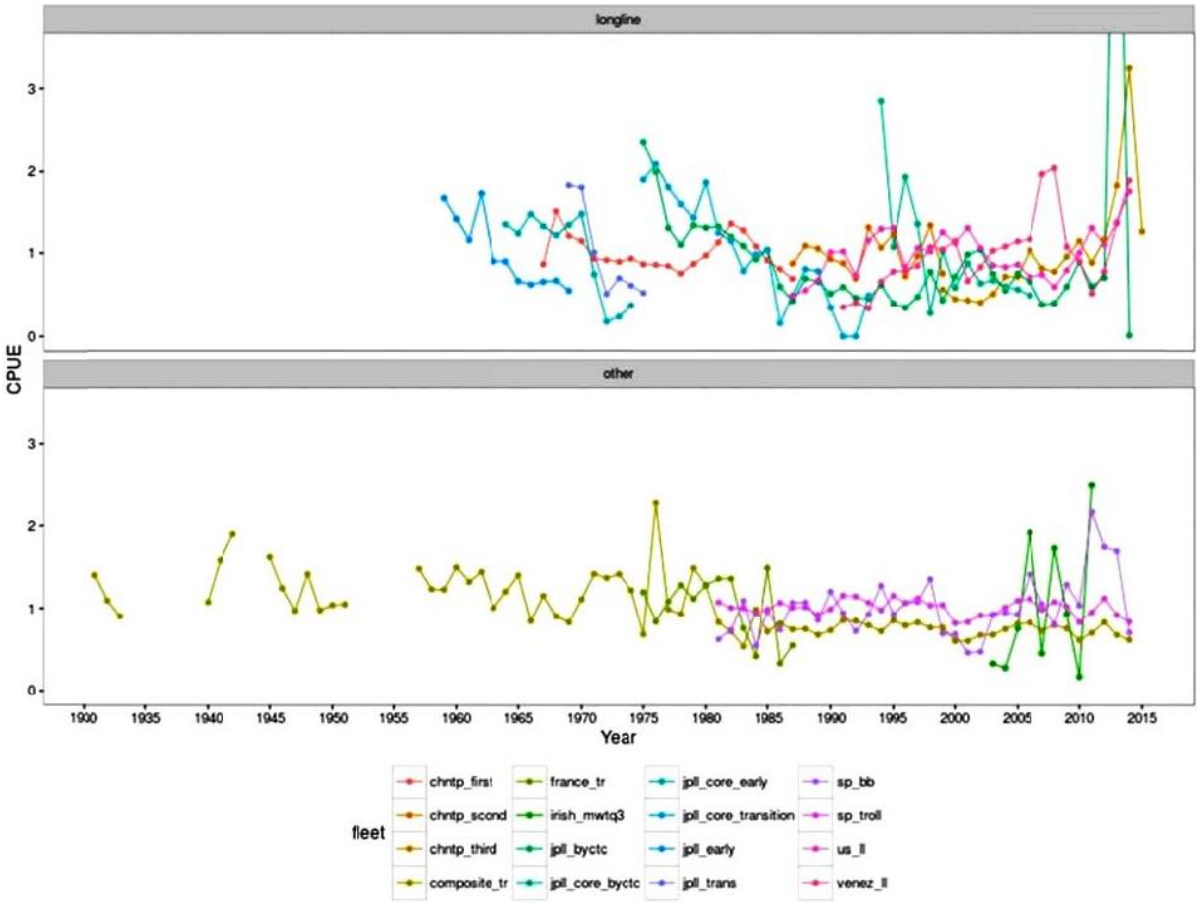

Figure 4. 5 The Standardised index trends of surface fisheries targeting albacore tuna in the North-east Atlantic region (acquired from ICCAT 2016 North and South stock assessment report)

Chapter 5: Overall Discussion

The overall aims of this research were to use otolith characteristics to improve understanding of the population structure of albacore tuna in the North Atlantic and to refine fisheries dependent estimates of abundance by incorporating vessel dynamics into the standardisation of catch per unit effort (CPUE) estimates.

5.1 Overview of study findings

In Chapter two, spatial variation in otolith shape was examined in juvenile albacore tuna captured in the eastern and western Bay of Biscay. Despite sample size limitations, the results showed that the mean otolith shape varied between catch locations. The findings indicated that juveniles feeding in the eastern and western Bay of Biscay differed in their environmental life histories. A canonical discriminant analysis based on Elliptical Fourier shape descriptors separated fish from the two areas with an accuracy of 72% for the eastern group and 75% for the western group. The results of this study support the hypothesis that juvenile albacore follow two alternative migration routes to the North-east Atlantic region to feed (Hue, 1980). The study also demonstrated the value of using a top-down approach to identify components within a stock, when the spawning locations of the stock are not known, as is the case for albacore tuna in the North Atlantic.

The main objective of Chapter three was to determine if albacore tuna caught in three different areas shared similar larval and pre-juvenile conditions using otolith microstructure and microchemical analyses. Results from the microchemical analyses supported the existence of multiple larval populations within the North Atlantic. Adult albacore captured near Venezuela could be distinguished from adults captured off the coast of Canada and juveniles captured in the Bay of Biscay using the composition of both the core and the post-core regions of the otolith. This suggests that these fish occupied a distinct larval environment. The results of the microstructure analysis showed that larval growth rates were similar across the three areas, indicating that even though the larvae may have been spawned in different areas, they experienced similar growing conditions and that the elemental differences observed between Bay of Biscay and Venezuela at the otolith core were caused by other exogenous factors, for example diet.

The aim of Chapter four was to evaluate the influence of vessel behaviour on CPUE estimates using hidden semi-Markov models and finite mixture models. Using observer data from the Irish mid-water pair trawl fishery, the hidden semi-Markov model was able

to distinguish fishing events from non-fishing phases with an accuracy of 87%. The model was used to categorise VMS-logbook records and to estimate the proportion of each trip spent fishing. In some years, predicted fishing proportion and CPUE were positively correlated indicating that catch rates were high during trips when a relatively high proportion of the time was spent fishing. However, in other years there was no correlation, possibly due to seasonal or spatial variability in distribution patterns and catchability. The two components that were previously identified in the data using finite mixture models were no longer present when fishing boat pairs were identified, and their catch combined. This proved to be the main reason for the two-component structure observed in the Cosgrove et al. (2014b) study highlighting the importance of accounting for the behaviour of the mid-water pair trawlers in the estimation of CPUE. When effort was expressed as total fishing time this reduced the variability in the catch rate standardisation compared to the model in which effort was expressed as total trip time.

5.2 Incorporating population structure into the management of albacore tuna

Chapters two and three provided insight into the population structure of albacore tuna. The observed variation in otolith chemistry suggests that during the spawning season (April – September), adults spawn in at least two distinct locations. The observed homogeneity in otolith growth rates at the larval core indicates that these locations share similar growing conditions (e.g. temperature and food availability). Although there is little to no information concerning albacore's life history between the lengths 2 cm and 38 cm, it is known that at length 40 cm, albacore juveniles begin migrating to feed in the productive waters of the North-east Atlantic (ICCAT, 2011). The variation in otolith shape observed between juveniles feeding in the inshore and offshore waters of the Bay of Biscay is as a result of the different environmental histories they experience during their lives.

At present, albacore tuna in the North Atlantic is managed as a single homogenous stock, and it is assumed that population dynamics and life history characteristics are uniform across the entire stock. The results from this thesis indicate that there is stock complexity in the North Atlantic albacore stock. Previous studies that compared otolith composition between juveniles caught in different locations in the Bay of Biscay also found evidence of stock complexity (Fraile et al., 2016; Sagarminaga and Arrizabalaga, 2010). In spite of

this, the assessment and management of the stock still conform to the unit stock assumption. This reflects the fact that there is no general consensus among fisheries scientists regarding the population structure of the species. For there to be a change in the assessment and management of the stock, additional evidence confirming the number of subpopulations present in the population is needed. Also, estimates of relative size, natural mortality, growth and productivity rates are necessary to characterise the subpopulations (Kerr et al., 2010b). This information can be obtained by first identifying the spawning locations and migration routes of the population and then sampling the subpopulations when they are on their spawning grounds in spawning condition or from mixed aggregations of the subgroups. The collection of this data is paramount to the progression of our present understanding of albacore's population structure and the improvement of its assessment and management which will be aligned with its biological structure.

Even though this information is not currently available, insight into the possible consequences of disregarding population structure can be investigated using management evaluation strategy (MSE) models (Kerr et al., 2017). The technique can be used to test hypotheses regarding connectivity, the spatial structure of the components and the overall stock composition using the biological and demographic information known about the subpopulations. For example, Kerr et al. (2010a) used an age-structured model with a substock component to model the spatial structure and connectivity of Atlantic cod (*Gadus morhua)* within the Gulf of Maine area and compared the results of the model to a single-stock management model. They also applied different fishing mortality levels to both models to examine the influence that spatial heterogeneity had on the productivity and yield of the stock. The authors found that the substock model had higher productivity and sustainable yield estimates than the single-stock model. They credited the higher productivity of the substock model to the incorporation of each subpopulation's demographic vital rates and recruitment dynamics and to the fishing mortality rate (F_{MSY}) being based on the productivity of each subpopulation and not one estimate for the entire stock which is the general assumption for the single-stock model. A similar approach could be performed on albacore to alert managers and stakeholders to the importance of aligning the management of the stock with its innate biological structure. To be able to generate this model for albacore tuna, knowledge on the subgroups' population dynamics, e.g. fishing mortality, recruitment, degrees of connectivity and mixing are needed.

Acquiring these parameters is crucial to ensuring that the biological structure of albacore tuna is properly reflected in its assessment and management. If the stock complexity is continued to be ignored, it may result in the over-exploitation of weaker components in the population and the reduced productivity, stability and resilience of the overall population which could lead to the collapse of the stock (Kerr et al., 2010b; Ying et al., 2011).

5.3 Standardisation of CPUE indices

Currently, many stock assessments are carried out on fishery dependent data. To account for the issues associated with this data source, standardisation of the catch data is a crucial step in ensuring the data reflects the abundance of the stock. At present, in the standardisation process and in stock assessments for most species, the variability in fishing effort is unaccounted for and instead the total length of the trip is used to represent the effort required to land the catch. The results from Chapter four highlight the importance of identifying vessel behaviour modes, specifically fishing, in vessel monitoring data using movement models and incorporating these modes into CPUE standardisation. VMS data (with logbook data included) utilised in movement models can improve the accuracy of fishery-dependent data and reduce the variability in CPUE standardisation. Charles et al. (2014) used VMS data in a hidden Markov model to develop effort estimates, based on behavioural states (retrieving, setting and steaming) in order to standardise the catch rates of the Gulf of St. Lawrence snow crab fishery. The authors found the standardised catch with fishing behaviour included agreed with fishery-independent estimates of snow crab abundance better than commercial CPUE estimates. This indicates that incorporating fishing patterns is important when using fishery-dependent data in CPUE standardisation.

5.4 Future studies and endeavours

5.4.1 Population structure

To enhance our understanding of albacore stock complexity in the North Atlantic, future work should attempt to collect samples from the Caribbean, where pre-juvenile albacore ($\leq$ 38 cm) have been caught (F. Arocha, personal communication, September 8, 2017). Otolith microchemistry analysis of the otolith core can be used to determine if the pre-

juveniles shared a common spawning site with fish caught later in life around Venezuela or the Bay of Biscay. Tagging studies of juveniles feeding in the inshore and offshore waters of the Bay of Biscay may provide vital information which can redefine the present understanding of albacore life history outside of the region (Childers et al., 2011; Prince et al., 1995). Also tagging of adults throughout the spawning period could help in identifying potential spawning sites in the North Atlantic. Conventional tags have been used for many years to elucidate the distribution of albacore tuna as well as to gather data on its total mortality and growth parameters, but their return rate has been shown to be low (Arrizabalaga et al., 2002). The use of miniaturised pop-up archival tags could be used to record and store information about albacore's movements and the ambient water temperature and then transmit this information via satellite at a predetermined time (Block et al., 1998). Pop-up tags have been shown to work well on albacore juveniles and subadults (Cosgrove et al. 2014a). The collection of sex-specific gonad samples throughout the fishing region has been outlined by ICCAT as a viable option to help identify potential spawning areas (ICCAT, 2016). Once potential spawning sites have been identified, larval surveys could be conducted to confirm the importance of the sites and to further our knowledge about this early larval stage. To collect tuna larvae samples, surveys are usually conducted using 333µm mesh Bongo nets with a 60 cm mouth opening (Reglero et al., 2012).

5.4.2 Fleet dynamics

Using VMS-logbook data to infer vessel behaviour and to quantify fishing effort from fishery-dependent data has been shown to be important in CPUE standardisation (Charles et al., 2014). One improvement to VMS data could be the collection of higher temporal resolution data. Both Charles et al. (2014) and Joo et al. (2013) showed that using VMS data with a shorter time interval can improve model accuracy. However, data storage would need to be large enough to adequately store these higher temporal resolution data. In future observer surveys, on-board camera systems could be used to improve the detail and quality of the observer data in the Irish mid-water pair trawl fishery. Electronic monitoring systems have been used to monitor different multispecies longline fisheries (Ames, 2005; Ames et al., 2007), crustacean fisheries (Hold et al., 2015) as well as bycatch incidents (Pasco et al., 2009). These systems are mostly used to identify various species and to collect measurement data on the catch; however, in the case of the Irish

mid-water pair trawl fishery, it could be used to increase monitoring efficiency on fishing vessels, especially in cases, where there aren't enough observers to monitor the trip for its entire duration.

In conclusion, this body of work has provided insight into the areas of population structure and fleet dynamics of the North Atlantic albacore tuna as well as in the standardisation process of CPUE estimates. This thesis reveals the work that needs to be done to continue learning about this invaluable species and to ensure its sustainable use and management.

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