BIOLOGY OF ALBACORE TUNA (THUNNUSALALUNGA, BONNATERRE 1788) OFF THE SOUTH WEST COAST OF SOUTH AFRICA

By

Stewart James Norman

Supervisors: Associate Professor Colin Attwood (UCT)

Dr. Francis Marsac (IRD)

Department of Biological Sciences

University of Cape Town

Rondebosch, Cape Town

South Africa 7701

September 2013

Minor dissertation submitted in partial fulfilment of the requirements for the degree of Masters of Science in Applied Marine Science

Contents

Plagiarism Declaration

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

Abstract

Albacore tuna (*Thunnus alalunga*) is a highly migratory species found in all of the worlds oceans. The origin of albacore south of Africa is in question. This species constituted 85% of catches of the South African commercial tuna fishing fleet from 2000-2009 and is an important species in supporting a large boat-based recreational fishery. Albacore were sampled at angling competitions, which offer a repeatable and cheap source of tuna, in the Western Cape of South Africa during 2012 and 2013. 119 Samples were used to determine a length-weight relationship ($M(g) = 0.0000184\ FL\ (mm)^{3.008}$) and to provide conversion ratios of various body measurements to fork length when total lengthwas not available. Visual examination of testes and ovaries indicated that albacore are not spawning off the coast of South Africa.A comparison between the ease of using sectioned sagittal otoliths and first dorsal spines indicated that otoliths were more precise for estimating the age of albacore. Von Bertalanffy growth parameters were estimated from 51 fish, ranging from 2-9 years old (L_∞=1100.07 mm; K=0.238 y^{-1}; t_0=-2.14). Stomach content analysis indicated that the mesopelagic squid *Lycoteuthis lorigera* is the most important prey item for South African albacore. $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis of albacore and yellowfin tuna (*T. albacares*) muscle tissue showed that they feed on prey that may depend on different primary producers but that the two species of tuna share the same niche in the southern Benguela food web. Trophic levels of 3.8 and 3.76 were assigned to albacore and yellowfin tuna respectively.

Acknowledgements

I would like to thank my supervisors Colin Attwood and Francis Marsac for facilitating the smooth running of this project. Without their connections and expertise I would never have had access to or understood such incredible fish. Thanks to the members of Department of Biological Sciences who showed such interest in the tuna that it motivated me to pursue this task and to take pride in my work. Thanks to Frédéric Menard and Michel Potier for hosting me in Sète and taking the time to impart some of their valuable knowledge and skills on to me.I would like to thank the AMS class of 2012/2013 for their friendship and support with special mention of Martin Emanual for all the perfectly timed breaks and entertainment he provided as well as his assistance during long hours in the lab. The South African National Tuna Association was invaluable in allowing us to sample fish caught during the Tuna National Competitions as well as the respective boat clubs for providing space to set up our field lab. Financial support was provided by the University of Cape Town's Marine Research Institute (Ma-Re) and the French Institut de Recherche pour le Développement (IRD). A final thanks to both my mum and dad for supporting me throughout my career at UCT.

List of Figures and Tables

Table 2.3: Regression statistics for first dorsal length (DL1), thorax girth (TG), body height (BH) and the length from the posterior operculum margin to the caudal keel (OCKL) related to fork length (FL), (n – sample size, a – x variable, b – y-intercept).

Table 2.4: Growth performance index for *Thunnus alalunga* from various stocks and localities, $\phi' = logK + 2\,logL_{\infty}$.

Table 2.5: Occurrence (O) and Frequency of occurrence (%FO), absolute number (Nabs) and wet weight (Wabs), percentage contribution by number (%N) and weight (%W), mean proportion by number (%MN) and mean proportion by wet weight (%MW), prey specific contribution by number (%PN) and prey specific contribution by weight (%PW) and prey specific index of relative importance (%PSIRI) of prey species or categories recovered from stomach contents (47 samples) (*Thunnus alalunga*).

Table 2.6: Mean ± standard deviation and (range) $\delta^{13}C$ and $\delta^{15}N$ stable isotope values for forty seven albacore tuna (*T. alalunga*) and sixteen yellowfin tuna (*T. albacares*). Stable Isotope Analysis was performed twice per tissue sample, at UCT and La Rochelle Universities.

Chapter 1.Literature Review

1.1 Introduction to Albacore tuna (*Thunnus alalunga*, Bonnaterre 1788)

The fifteen species of tuna that roam the world's oceans are separated into five genera and comprise a monophyletic clade of the family Scombridae. Theirsister group in this family are the bonitos. Extant members of these two groups first appear around 60 million years ago (mya) (Carroll 1988). Albacore (*Thunnus alalunga*) is one of eight species of tuna in the most advanced genus of the subfamily (also known as a Tribe)*Thunnini* Starks, 1910. The genus *Thunnus* South, 1845,contains the three tropical species of tuna - the yellowfin tuna (*T. albacares*), blackfin tuna (*T. atlanticus*) and longtail tuna (*T. tonggol*) (Collette, Reeb and Block 2001), and also the five larger species of tuna that have been able to colonise cooler waters - the Atlantic bluefin tuna (*T. thynnus*), Pacific bluefin tuna (*T. orientalis*), southern bluefin tuna (*T. maccoyii*), albacore tuna (*T. alalunga*) and bigeye tuna (*T. obesus*) (Collette, Reeb and Block 2001).

The early tunas lived in a large circumtropical waterway known as the Tethys Sea (Dickson and Graham 2004). About 25mya paleoceanographic changes, induced by tectonic plate movements, affected the radiations of tunas and bonitos. Modern ocean thermohaline and gyre circulation began (22mya) as a result of the Tethys Seaway closing (25 mya). The filling in of the Isthmus of Panama cemented the blockade between the tropical Indo-Pacific and Atlantic Oceans (3 mya) thus limiting movement between these water masses to the area south of Africa (Ely et al 2005). Progressive cooling of the ocean began ~50mya. Accentuated vertical thermal stratification and an increase in high-latitude upwelling and productivity contributed to current tuna distribution by opening up new niches and expanding food webs (Dickson and Graham 2004).

To gain access to and exploit these areas tunas evolved a unique mode of swimming, known as 'Thunniform', that allowed development of an exceptional integration of continuous swimming and physiological performance (Dickson and Graham 2004). Thunniform swimming is defined by minimal lateral body undulation and the concentration of thrust production at the rapidly oscillating, lunate caudal fin (Altringham and Shadwick 2001). This feature of tunas coupled with a capacity for effective regional endothermy and elevated aerobic capacity allowed for an expansion of their latitudinal and vertical range.

1.2 Tuna Fisheries in South Africa

Tuna have since colonised all of the world's oceans, in cold waters as far as latitudes 50°S and 60°N as well as warm tropical waters. A spotlight has been aimed at the region south of Africa in an attempt to determine the origin of the fish either dwelling in or moving through the area. The region is one of the most productive in the world and is the meeting point of the Agulhas (warm western boundary) and Benguela (cool upwelling) currents.It is also the corridor between the Atlantic and Indo-Pacific Oceans for tuna of several species. If it proves that there is considerable mixing between the Atlantic and Indo-Pacific Ocean populations of tuna as opposed to distinct stocks then a major reform of fisheries management principles would be required to accommodate a single, pan-ocean stock. Currently the Atlantic, Indian and Pacific Ocean tunas are managed separately. There are five major tuna fishery management bodies: the International Commission for the Conservation of Atlantic Tunas (ICCAT), the Indian Ocean Tuna Commission (IOTC), the Western Central Pacific Ocean Fisheries Commission (WCPFC), the Inter-American Tropical Tuna Commission (IATTC) and the Commission for the Conservation of Southern Bluefin Tuna (CCSBT). South Africa is a member (or cooperative party) of three of these commissions: ICCAT; IOTC and CCSBT.

Tuna were once thought to be infrequent visitors to the South African coastline and consequently research on tunas in South Africa lagged behind that in the rest of the world. The first records of tunas from South Africa were made by Gunther (1860) but even by 1927 the list of tunas known off the Cape was vastly incomplete (Shannon 1987). There are 7 species of tuna that occur within or at the fringes of the South African exclusive economic zone, namely:*Thunnus alalunga* (longfin/albacore), *T. albacares* (yellowfin), *T. obesus* (bigeye), *T. maccoyii* (southern bluefin), *T. thynnus* (bluefin),*Katsuwonus pelamis* (skipjack) and *Allothunuus fallai* (slender tuna). By 1941 there were frequent reports of tuna in False Bay but the species was not identified. The end of World War II saw the emergence of sports fishing in the Cape (Horne 1959). By 1952 several thousands of troll-caught tuna were landed during summer off Cape Point and Hout Bay (Talbot and Penrith 1968, Penney and Griffiths 1999). 1960 marked the first development of a small tuna longline fishery in South Africa (Talbot and Penrith 1968). The fishery recorded catches for 1962 and 1963 of around 2000 t but soon dissolved inthe mid-1960's due to economic reasons and the poor quality of fish landed (Nepgen 1971, Shannon 1987).

The Department of Sea Fisheries conducted exploratory fishing for tuna off the South African West coast in the early 1960's (de Jager et al 1963). Although the recreational fishery continued, there was almost no commercial interest in the exploitation of Benguela tunas from South Africa until much later (Shannon 1987).

Renewed interest in a commercial tuna fishing industry was prompted in 1979 due to the discovery of an unusually high prevalence of yellowfin tuna on the western edge of the Agulhas Bank, with catches exceeding 9000t that year (Sea fisheries report no. 47, 1979). The rush was short-lived as this species didn't reappear in the same numbers the following year.What came of the appearance of yellowfin tuna however was a sustainable surface

pole/baitboat fishery that focused its efforts on albacore tuna. Effort shifted to albacore in 1980 and catches have averaged over 4500 t from 1980 – 2011 (ICCAT Statistical Bulletin 2013). The baitboat fishery operates seasonally when albacore are present in coastal waters from October to May and targets mainly juvenile and sub-adult albacore tuna (70-90cm FL) (ICCAT Report 2008). The migratory yellowfin tuna again became abundant in waters around the Cape during the first decade of the 21st century (Kerwath et al 2012), and are actively targeted when they are seasonally available (Newcombe 2011).

Whereas South Africa was slow to exploit its tuna, internationally there has been commercial interest in tuna species found in South African waters since the early 1950's, from Japan and Taiwan since the late 1960's (Kroese 1999). Both nations initially employed traditional longlining methods to target albacore but by the late 1970's had shifted their efforts to target bigeye tuna using deep longlines (Kroese 1999). There are currently five participant countries actively fishing for southern Atlantic albacore, the Chinese Taipei, South Africa, Namibia, Brazil and Uruguay.They share 21 000 t of the total allowable catch (TAC) set up for the south Atlantic stock by ICCAT. For Japan an albacore-by-catch limit of 4% of the total weight of their bigeye-targeting longline catch has been set.

Presently, the South African commercial tuna fishery comprises the longline, pole/baitboat and rod and reel fisheries and a boat-based recreational fishery (Department of Agriculture, Forestry and Fisheries 2012). The longline fleet operates in the offshore waters of the Agulhas Current along the entire South African continental shelf (Sauer et al 1997, Sauer et al 2003) and comprises a total of 26 tuna long-term rights holders (Newcombe 2011).The baitboat fishery sector comprises 137 active vessels that are greater than 10 m in length (Kerwath et al 2012).Baitboats operate out of various ports up to 1000km off the south and west coasts of South Africa and Namibia (Newcombe 2011, Kerwath et al 2012). Albacore

concentrate around hydrological features such as underwater seamounts and canyons and are found associated with meteorologically induced fronts and oceanic fronts (Laurs et al 1984, Penney et al 1992). The baitboat and longline fisheries target albacore that occur in 4 main areas of the Benguela region: Vema Seamount off Namibia, Tripp Seamount south of Luderitz, South Bank south of Hondeklip Bay and the Cape Canyon (Penney et al 1992). The recreational sport fishery consisted of roughly 200 tuna-going vessels in 1995 but grew substantially to comprise an estimated 8 000 vessels and in excess of 31 800 anglers by 2008 (Newcombe 2011). Sports fishers in Sodwana Bay, Algoa Bay and the Cape Peninsula often trail trawlers and longliners in search of tuna that are attracted to discards.

The South African tuna fishery is the second largest in the South Atlantic with landings around 5000t per annum. Baitboats contribute approximately 4000t of albacore (Kerwath et al 2012). By far the largest exploiter of albacore in the South Atlantic remains the Taiwanese longline fishery, accounting for 46 – 90% of total landings between 1970 and 2004 (Kerwath et al 2012). Other tuna species from the south Atlantic contribute relatively small amounts to the total tuna catch by the South African tuna fishery (Figure 1.1).

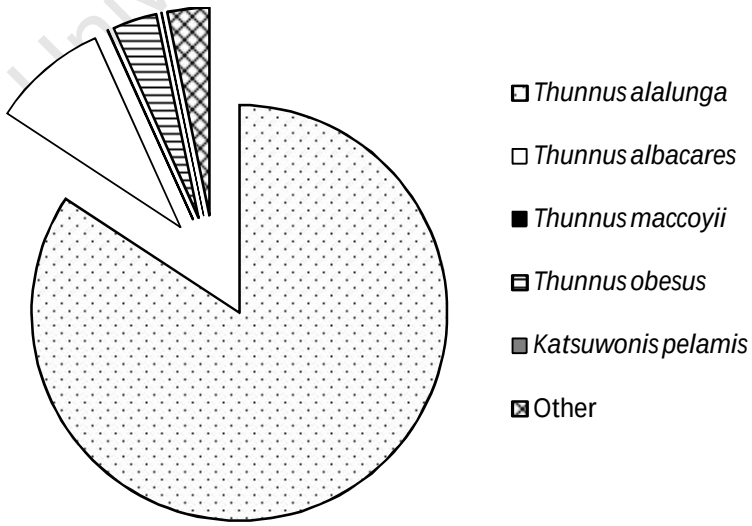

Figure 1.1: Relative catch composition of tunas by the South African tuna fishery in the Atlantic Ocean over the years 2000-2009.

Albacore found in the waters off the Cape of South Africa are proposed to originate from the south Atlantic stock (Penrith 1963,Yeh et al 1996, Penney et al 1998,).However, there is likely some degree of mixing of immature individuals during winter and mature fish throughout the year, between the Atlantic and Indian Oceans (Morita 1978, ICCAT Report 2011). Mixing may also occur via larval transport into the Atlantic Ocean from the south-west Indian Ocean (Fonteneau 2004). According to the Indian Ocean Tuna Commission (IOTC) report for 2012 the juvenile albacore caught off South Africa's Atlantic coastline may originate from both the north east of Brazil and the Indian Ocean. The IOTC have assumed a "one pan-ocean stock for management purposes". However, the current stock assessment undertaken by ICCAT and the IOTC still considers separate stocks east and west of 20°E.

1.3Morphological Traits of Albacore Tuna (*Thunnus alalunga*)

Albacore tunahas long pectoral finsthat can reach greater than 30% of fork length in individuals longer than 500 mm. Juvenile albacore however have relatively short pectorals and can be confused with juveniles of *T. obesus*. It has fewer gill rakers (23-31) than the bluefins and southern bluefin (31-43) and is the only species in the genus *Thunnus* that has the spleen on the right side of the viscera (Collette, Reeb and Block 2001). The body is wide in the middle, tapering toward either end and covered with small cycloid scales. They lack spots or stripes, distinguishing them from other tuna species, and are metallic dark blue on the dorsal side and silvery white ventrally.An iridescent blue band runs along their sides in live fish but quickly fades once fish are caught. The first dorsal fin is a deep yellow, the second dorsal and anal fins are a lighter yellow. Features that differentiate this species from the other *Thunnus* species are highlighted in figure 1.2.

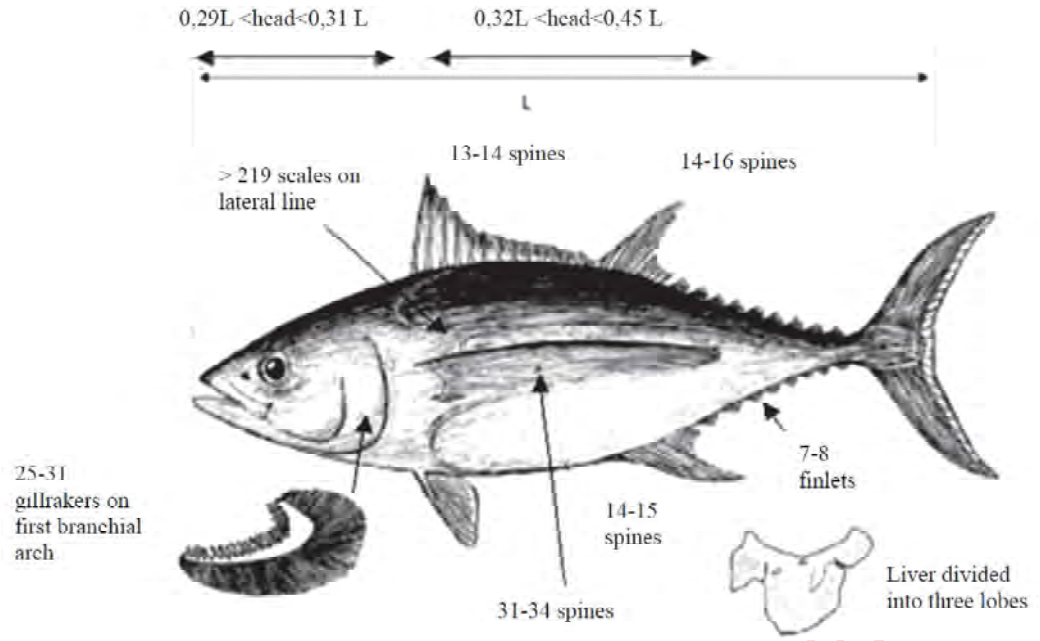

Figure 1.2: Most striking features of albacore tuna, *Thunnus alalunga* (Santiago 2004).

1.4Distribution: Atlantic Ocean Stock Structure and Migration Patterns

Albacore tuna are widely distributed in all oceans, including the Mediterranean Sea. This species has been found from 42°N to 32°S in the Atlantic, 0° to 40°S in the Indian Ocean, and 50°N to 45°S in the Pacific (Gibbs and Collette 1967, Collette, Reeb and Block 2001), although abundance is relatively low in equatorial regions (Lewis 1990). Albacore are a temperate species of tuna, favouring subtropical ocean waters of 16° – 20°C (Penney et al 1998), but appear to be differentially distributed depending on their life-history stage (Chen et al 2005).

Spawning occurs in equatorial regions where water temperatures exceed 24°C (Schaefer 2001). Reproduction studies by Beardsley (1969) and Koto (1969) led to the identification of two distinct spawning locations for the Atlantic Ocean: the Sargasso Sea in the northern hemisphere and an area centred around 10°S off the coast of Brazil in the southern hemisphere. Bard (1982) suggested a third spawning location in the central south Atlantic.

Subsequent studies of the spatial distribution of adult albacore derived from Japanese longline fishery data (Shiohama 1971, Uozumi1996) and from larval distribution studies(Ueyanagi 1971) supported the earlier conclusions on location of spawning.

For Atlantic albacore three stocks are recognised, the northern and southern Atlantic populations and the Mediterranean population. Little is known about albacore migration patterns for the south Atlantic and the Mediterranean Sea. Some degree of mixing between the north and south Atlantic populations and north Atlantic and Mediterranean populations most likely occurs (Arrizabalaga et al 2007).

From recent genetic confirmation using microsatellites (Takagi et al 2001) and blood groups (Arrizabalaga et al 2004) it is hypothesised that two distinct populations of albacore occur in the Atlantic Ocean on either side of 5°N latitude. Genetic studies of albacore caught in the Gulf of Guinea (south of 5°N) show these fish have greater similarity to the northern stock than to the southern, implying that the limit is either father south or that there is some degree of mixing between the populations (Arrizabalaga et al 2004, Arrizabalaga et al 2007). The Mediterranean albacore stock is considered independent from the Atlantic stocks. Bard (1981) presented evidence of different morphometric characteristics between Atlantic and Mediterranean stocks and Megalofonou (2000) showed that there was a significant difference between growth parameters for Mediterranean and north Atlantic albacore. Arrizabalaga et al(2004)noted from tag-recapture analysis thata single fish migrated from the north Atlantic into the Mediterranean Sea, but the information was insufficient to support any hypothesis on the possible interchange between those two populations (Ortiz de Zárate and Cort 1998).

For North Atlantic albacore, the migration routes of both juvenile and adult fish have been resolved(Aloncle and Delaporte 1973,Harvard Duclos 1973, Bard 1981, Ortiz de Zárate and Cort 1998, Alonso et al 2005).

Although extensive research into south Atlantic albacore populations has not been carried out there is information available to assess the stock structure, migration routes and potential mixing of south-east Atlantic and Indian Ocean albacore.

Southern albacore migrate annually through their Atlantic distribution range between 10°S and 40°S. Nepgen (1971) noted that juvenile and sub-adult albacore are present in the Benguela region throughout the year.They migrate locally along the west coast feeding at upwelling and topographically induced fronts (Penney et al 1992). Adults of the population occur mostly off Brazil, Argentina and Namibia (Penney et al 1992). Albacore catches by gear (1985-2000, Figureure 1.3) indicate a preponderance of juvenile albacore in the southern Benguela (caught by the South African pole and line/baitboat fishery) and adult albacore along the east coast of South America (caught by international longline fisheries).

The early work of Penrith (1963) describes a strange break in the distribution of albacore around the South African coastline. He noted that this species occurs from St. Helena Bay (32°48'S;17°59'E) to Danger Point (34°36'S;19°18'E) along the west and south-west coastline but then disappears offsouth coast. Albacorethen only reappear off the coast of Kwa-Zulu Natal around Durban (29°45'S;31°2'E). This led to the hypothesis that albacore found in the waters off the Cape are of Atlantic origin as the break in distribution constitutes almost the entire south coast of South Africa.

Penney et al(1998) synthesised catch distribution maps for tuna fisheries of the Atlantic Ocean (ICCAT Albacore Species Group1996), the Indian Ocean (Ardill 1995), the Japanese longline fishery (Uozumi 1996), the Taiwanese longline fishery (Chang et al 1996) and the South African baitboat fishery (Penney et al 1992) to produce a global catch distribution map for albacore. They used this information coupled with morphometric measurements of albacore caught by the South African baitboat fishery as the basis for comparative analyses of

south-east Atlantic and Indian Ocean albacore. Based on distribution patterns, Penneyet al(1998) concluded that the Agulhas Current acts as a thermal barrier to movement of fish between the two oceans. The current penetrates westwards toward Cape Point coming off the south-eastern edge of the Agulhas Bank off southern Africa, where temperatures can exceed 25°C (Beckley and van Ballegooyan 1992). Based on the thermal characteristics of the Agulhas Current, juvenile albacore, anatomically constrained to surface waters, would be unable to cross into the Indian Ocean. It is physiologically possible that adult albacore may dive to 200 m or more into cooler water to enter the Indian Ocean, but as yet there is no evidence of this.

Supporting the hypothesis that the Agulhas current prevents movement between the south Atlantic and Indian Oceans is tag-recapture information published by the South African Oceanographic Research Institute(van der Elst and Bullen 1987).By that stage a total of 291 albacore had been tagged. The majority were tagged to the west of Cape Point (at approximately 34°20'S, 18°20'E).22 (7.6%) were recaptured (average time at liberty = 286 days, average distance travelled = 321 km), but all recaptures were made to the northwest of the tagging area.

Morphometric comparisons between western, central and eastern Indian Ocean albacore andsouth Atlantic Ocean albacore (Yeh et al 1996, Penneyet al 1998) yielded the following relationships. Central and western Indian Ocean albacore show high morphometric similarities.Eastern Indian Ocean albacore show differences from the central ocean stock. Atlantic Ocean albacore show strong morphometric differences with Indian Ocean albacore and those differences strengthen with increasing distance from the Atlantic. Further work by Yeh et al (1997) demonstrated a distinction between south Atlantic and eastern Indian Ocean albacore through mitochondrial DNA sequence analysis.

Prompted by suggestions made by Koto (1969), Morita (1978) analysed Japanese longline vessel catch statistics and length data for the years 1965 – 1975, and formed an opposing hypothesis on the origin of albacore in South African waters. He suggested that there is a possible intermigration of albacore between the Indian and Atlantic oceans during the winter season and that this phenomenon is dominated by 4^{+} year old fish.

In a recent description of Indian Ocean albacore fisheries and stocks by Fonteneau (2004) the hypothesis of albacore found in South African waters being only of Atlantic origin is again disputed. Based on his interpretation of fisheries data, coupled with environmental data, he proposes a potential spawning ground east of Madagascar (5 to 15°S) where sea surface temperatures can exceed 25°C. If this were the case then there is a strong possibility that larvae and juveniles could drift around the Indian Ocean sub-tropical gyre via surface counter currents and move south-westwards towards the most northern limit of the subtropical convergence finding their way as far as Namibia (Fonteneau 2004).Figure 1.3 was presented by Fonteneau (2008) during the IOTC working party to suggest that there is no boundary between the southern Indian and southern Atlantic oceans.

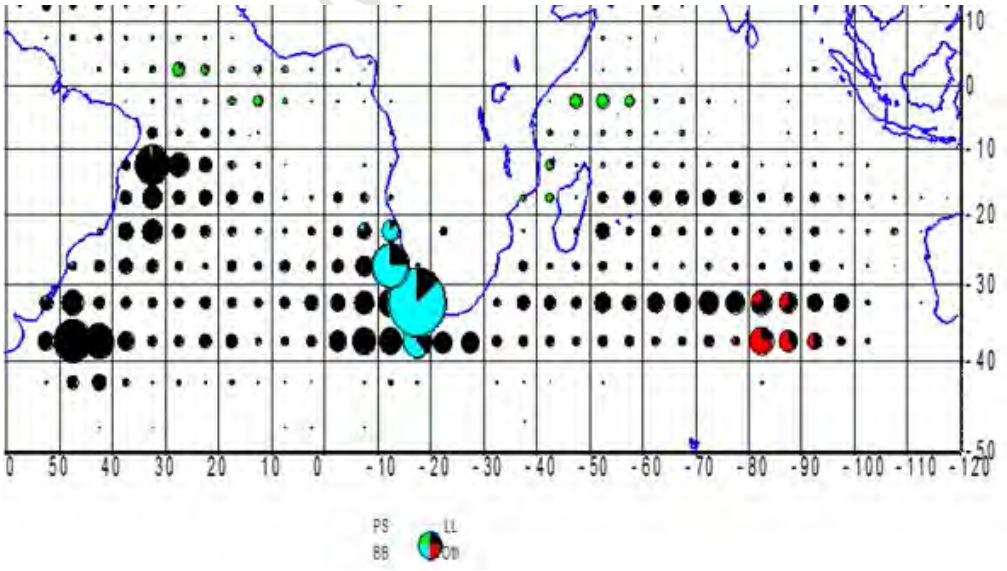

Figure 1.3: Albacore catches by gear 1985 – 2000 (Grey: pole and line, black: longline) (Fonteneau 2008).

Chen et al (2005) showed for Indian Ocean albacore that different developmental stages preferred different oceanographic conditions, with mature fish occupying the area north of 10°S, mature-spawning fish dominated between 10°S and 30°S, with immature fish constituting the developmental stage found south of 30°S. Tuna species are widely distributed and use current systems to segregate by size and usually migrate across current systems during changes in developmental stage (Nakamura 1969).

The current working hypothesis would be that the Atlantic and Indian Oceans as the sources for albacore found in the waters off the coast of South Africa. Tag-recapture studies, such as those recently applied to Broadbill swordfish, *Xiphias gladius*, (West et al 2012), and more sophisticated stock identification, is required to accurately identify the origin of these migratory tunas. Until such a time as this is carried out, this issue remains open to debate.

1.5Biology of *Thunnus alalunga*

The biological parameters that underpin successful stock assessment include age at first maturity, spawning frequency, recruitment success, growth and mortality. There is inter- and intra-specific variation in the biology of tunas. Specific evaluation of individually defined stocks is required for their successful management. There is currently a good understanding of tuna physiology and ecology but as fishery exploitation levels shift and the global climate changes there is a need to explore the effect of anthropogenic changes on tuna biology.

1.5.1 Spawning/reproduction

Albacore are dioecious and do not show sexual dimorphism in their colour pattern or external morphological characteristics (Schaefer 2001, Alonso et al 2005). Albacore exhibit a directed seasonal migration to discrete spawning locations and a spatiotemporally confined spawning pattern as do the Pacific and southern bluefin tunas (Schaefer 2001). Temperatures in excess

of 24°C, a mixed layer depth of about 50m and a deep thermocline appear to stimulate maturation and spawning behaviour (Ueyanagi 1969, Alonso et al 2005). Seasonal northward and southward movement of the 24°C isotherm results in pronounced seasonal spawning in subtropical regions during austral and boreal summer months. Tunas have very high life time fecundities, estimated at 2-3 million eggs per female for albacore (Postel 1964), although information on spawning behaviour and spawning frequency, from which this estimate should be partly derived, is limited for albacore, as the species has not been successfully kept in captivity (Schaefer 2001).

1.5.2 Growth

Albacore do not grow to the same size as the larger tunas.Collette and Nauen (1983) estimated a maximum length of 1270 mm in the Atlantic whilst Le Gall (1974) predicted a maximum lifespan of 15 years and length of 1300 mm. Bigeye tuna,*Thunnus obesus*, that shares a similar distribution to albacore tuna, can grow up to 2500 mm total length (Reiner 1996) and the maximum recorded age is 11 years (Froese and Pauly Eds. 2006). The pan-tropical yellowfin tuna can attain a maximum length of 2390 mm (*International Game Fish Association*) and live for up to 8 years (Froese and Pauly Eds. 2006).

The estimation of the age of a fish, or a measure of growth over a known period of time, is necessary to determine its growth rate. There are various age-determination techniques using different hard part structures of a fish.Most common are sagittal otoliths, dorsal fin spines, scales and vertebra. The accuracy of age determination varies depending on the technique, sample size, the size range of fish sampled and the temporal length of the study. Numerous studies have estimated the growth of the three Atlantic Ocean albacore stocks with varied results (Table 1.1).

Table 1.1: von Bertalanffy's growth parameters for *Thunnus alalunga* obtained by different studies for the equation $L_t = L_\infty * (1 - e^{(-K*(t-t_0))})$, where L_t is the fork length (FL) at age t, L_∞ is the theoretical asymptotic fork length, K is the Brody growth coefficient, t is the age in years and t_0 is the theoretical age of a zero length fish.

Author	Stock	Growth parameters			N	FL range (cm)	Methodology
		L_∞	K	t_0			
Bard (1981)	North Atlantic	124.74	0.23	-0.99	352	46-113	Spines
Lee and Yeh (1993)	South Atlantic	142.8	0.145	-0.67	353	85-117	Spines
Megalofonou (2000)	Mediterranean	94.7	0.258	-1.35	1136	57-92	Spines
Lee and Yeh (2007)	South Atlantic	147.5	0.126	-1.89	344	51-130	Spines
Cheng et al (2012)	Southern Indian Ocean	113.7	0.194	-8.39	106	97-120	Spines

ICCAT currently applies the parameters estimated from Bard (1981) for assessment of both north and south Atlantic albacore stocks. With the variation between distinct populations of tuna it would be more accurate to apply estimates of growth to the south Atlantic stock based on an assessment of that stock.

1.5.3 Length-weight relationship

A length-weight relationship estimated from a large sample size, taking into account seasonal variation and specific to a defined region or population is useful for monitoring the condition of a fish stock. Accurately measuring the weight of the catch at sea can be difficult due to unstable conditions and weight is affected if the fish has been eviscerated.It is easier to measure the length of each individual caught and the number of those individuals. Using an applicable length-weight relationship it is possible to determine the weight of the catch.

Penney (1994) determined the parameters for a length-weight relationship for albacore sampled off the west coast of southern Africa. Based on a sample size of 1008 fish ranging from 46-118 cm (FL) he estimated that: Weight (kg) = $1.3718 \times 10^{-5} \times FL^{3.079}$.It is possible that this relationship, used currently in stock assessment for the south Atlantic, is out-dated.With the speculation regarding the source of albacore found in the waters off the coast

of South Africa and the variation in length-weight parameters obtained by various studies (Table 1.2) it is important to re-evaluate the parameters for the albacore caught off the South African coast.

Table 1.2: Length-weight relationship parameters obtained by different studies, parameters fit a power curve in the form $(kg) = a * FL\ (cm)^b$.

Author	Stock	Growth parameters		N	FL Range (cm)
		a	b		
Megalofonou (1990)	Mediterranean	3.12 x 10-05	2.880	998	57-92
Santiago (1993)	North Atlantic	1.34 x 10-05	3.107	714	42-117
Penney (1994)	South Atlantic	1.37 x 10-05	3.097	1008	52-118
Hsu (1998)	Indian Ocean	5.69 x 10-05	2.751	2499	46-112

1.5.4 Maturity

Bard (1981) estimated that 50% of fish in a given albacore population are mature at 900 mm fork length or age 5, this estimate is combined for both males and females as no difference was noted between the two sexes. Compared with *T. obesus*, *T. albacares* and *K. pelamis* that mature at ages 3.5, 2.8 and 1.5 years respectively (Fromentin and Fonteneau 2001) albacore mature later and live longer, with an estimated maximum age of 15 years (LeGall 1974). Comparably southern bluefin tuna (*T. maccoyii*) are a truly long-lived species, only maturing at 8 years of age and 1300 mm fork length (Fromentin and Fonteneau 2001) and living up to 41 years of age (Gunn et al 2008).

1.5.5 Sex-ratio

Since tunas show no sexual dimorphism in any external characteristics (Schaefer 2001) most experimental determination of sex ratios are based on the macroscopic examination of gonads. In small, immature individuals it is difficult to assign a sex based on macroscopic examination. For most tuna species, including *T. alalunga* and *T. albacares*, the overall sex ratio does not deviate from 1:1 (Schaefer 2001). However there can be a prevalence of males

of these two species in larger size classes. The likely reason for this is a higher natural mortality in females once they become sexually mature.

Otsu and Sumida (1968) found in the albacore longline fishery based in American Samoa from 1954-1965 that males greatly outnumbered females in size classes larger than 900 mm and averaged 10 to 60 mm longer than females. Schaefer (1998) describes a more complicated scenario for *T. albacares* where for the size class 500 to 549 mm a deviation from 1:1 expected sex ratio was observed (41.9% males). He hypothesised that this may be due to different growth rates between sexes but then goes on to say that the absence of females in larger size classes may be caused by differential natural mortality, possibly linked to sexual maturity, instead of different growth rates.

1.5.6 Diet

Tuna are opportunistic predators (Menard et al2006). Fish predation has been described as a non-selective process controlled by the availability of prey and predator-prey size ratios (Shin and Cury 2001, Shin and Cury 2004). Tunas are pelagic predators that represent a high biomass in open-sea ecosystems (Menard et al 2006), where, compared with coastal ecosystems there is relatively low production. Continuous swimming in schools is a mechanism of tuna feeding success in open-sea ecosystems where their food sources are widely and inconsistently distributed (Sund et al 1981). There are two main feeding actions among pelagic species: particulate and filter feeding.Particulate feeding requires the visual detection of prey (Menard and Marchal 2003).

Tuna have high swimming performance and can either chase down individual prey or track or find schools of fast swimming epi-pelagic fish such as sardines or anchovies (Menard and Marchal 2003). It was shown for tropical tuna that mean and maximum prey size increases

with increasing predator size, minimum prey size however varies little with tuna size indicating that large tuna continue to feed on small prey (Menard et al 2006).

Tuna feed mainly during the day by particulate feeding and have the capability to filter feed at night using effective gill rakers Filter feeding is more energetically expensive and not competitive compared to particulate feeding (Menard and Marchal 2003). Tuna prey is primarily micronekton organisms that are ubiquitous and exhibit predictable, vertical migrating behaviour in the water column (Menard et al 2006). They also feed on schooling stocks of sardines, anchovies, mackerel and squid (Alonso et al 2005).

1.5.7 Physiology

Albacore are able to increase the efficiency of their muscles through the adaptation of counter-current heat exchangers, *rete mirabile*, that enable them to reduce heat loss generated through muscular activity (Alonso et al 2005). Between 11.5 and 18°C albacore can maintain their red muscle at an estimated temperature of 20.7°C (Graham and Dickson 1981). Thermoregulation enables extended migration and colonisation of both vertical and horizontal habitats. Sustaining high metabolic activity and swimming speeds, juveniles at 57 $cm.s^{-1}$, adults slower than 45 $cm.s^{-1}$ (Dotson 1976), places a great demand on oxygen consumption. Bard (1982) suggested that albacore are physiologically constrained to water where the oxygen content does not drop below 2.5 $ml.l^{-1}$.

1.6Research needs on albacore tuna in South Africa

Future studies on albacore tuna in South Africa should focus on their origin and migration. The Agulhas current retroflection zone may act as a mixing zone for the Indian and Atlantic Ocean albacore stocks. Depending on the rate of interchange between the two stocks theywould need to remain distinct or be combined and studied as a single population. Genetic signatures, carbon stable isotope signatures,biological parameter analyses and the use of

parasites as biological tagscan provide the information required to differentiate fish populations.

An integrated stock assessment that incorporates the biological characteristics and age-structure of the stock of albacore is important for the management of the South African commercial tuna baitboat fishery, for which albacore constitutes 85% of catches. Anaccuratelength-weight relationship for the conversion of catch in number to catch in weight is needed for this commercial fishery.

For most tunas there is very little information available on their reproductive biology (Schaefer 2001). Spawning distributions, maturity and fecundity schedules, and size specific sex ratios are essentially nonexistent for albacore tuna. These parameters need to be investigated and incorporated into statistical assessment models for a species that is targeted by large-scale commercial fisheries in all three major oceans of the world.

Understanding the trophic ecology of albacore either residing in, or migrating through, South African waters will be of use in ecosystem models and may help in identifying the origins of this tuna. Diet studies and stable isotope analysis in the southern Benguela ecosystem and Agulhas retroflection zone at regular intervals are required as these areas are subject to unusually long environmental variation and moderate fishing pressure.

The bulk of research on albacore tuna in the south Atlantic and region of South Africa was done before the turn of the century, there is thus a strong need to update our knowledge on the biology and movement of this species. Restarting and maintaining a monitoring program of tuna catches in South Africa will allow comparison to historical knowledge and set-up a database for the long term analysis of such commercially important species.

Chapter 2. The Age, Growth and Feeding Ecology of Albacore Tuna (*Thunnus alalunga*) off the south west coast of South Africa

2.1 Introduction

According to the ICCAT recommendations and resolutions adopted at the 2011 commission meeting there remains "considerable uncertainty" about the most recent stock status of south Atlantic albacore (ICCAT Circular # 5058/2011). Based on the 2011 assessment that took into account eight scenarios, the median estimate of Maximum Sustainable Yield (MSY) was 27 964 t.The stock is considered to be overexploited and annual catches since 2004 havebeen below MSY (2010 catch, 18 900 t). The estimate of spawning stock biomass (SSB) is below SSB_{MSY}, SSB_{2011}/SSB_{MSY} = 0.88 (range, 0.55-1.59). The current rate of fishing is above F_{MSY}, $F_{current}/F_{MSY}$ is estimated at $1.07y^{-1}$(range, 0.44-1.95). Most recent Total allowable Catch (TAC) levels have been set at 24 000 t for 2012 and 2013, with a 50% chance of stock recovery within 5 years if this limit is not exceeded.

These recommendations were made based on the assessment of catch, effort and size data up until 2009. The analysis of catch per unit effort (CPUE) data relates catch to abundance and effort (Maunder et al 2006). Standardisation of CPUE is carried out so that the catchability co-efficient (q) of a stock can be assumed to remain constant over time. Factors that affect q include the dynamics of the targeted population or fishing fleet, the efficiency of fishing, directed species targeting and environmental fluctuations (Maunder et al 2006). The traditional analysis of standardised CPUE data is problematic, with technological advancements and improved catch rates, management regimes for tuna fisheries need to be reviewed (Newcombe 2011). For species that are selectively targeted at different ages the

importance of knowing the age-structure of the stock increases as different year groups are targeted differentially. Additionally the various age-groups are either more, or less vulnerable to the various fishing gear/techniques applied by the fishing fleets. The South African baitboat industry targets juvenile albacore (<5years) and has shown a stable pattern for the last decade (Kerwath et al 2012). This species is also targeted at different ages by longliners and the recreational fishery. There is a need to obtain age and growth information to estimate the survivorship at different ages. Population dynamic models, such as integrated stock assessments, incorporate biological information and define how a population and its age–structure change over time. They provide a more thorough assessment of stock status that facilitates effective management (Newcombe 2011). Biological data is essential for more accurate models.

Farley and Clear (2008) evaluated the use of otoliths and dorsal fin spines for ageing albacore tuna caught off Australia's east coast. Their evaluation led them to conclude that both structures can provide reproducible counts and that the agreement rate is high between structures for ages 1-7 but decreases with increasing age. In the current study the first dorsal spine from the first dorsal fin and sagittal otoliths were removed from fish and were sectioned for age estimation.

The von Bertalanffy growth model predicts body length as a function of age, most commonly the measure of fork length. In certain cases it is difficult to obtain an accurate measure of an individual's fork length such as when the fish has been eviscerated. The application of suitable conversion ratios to allow for the calculation of fork length in those cases is then required. The measurement of first dorsal length is related to fork length to provide a conversion ratio to obtain the measure of fork length when it is not available.

The growth rate of an individual is affected by environmental and physiological factors within their habitat ranges (Lehodey and Leroy 1999). Growth can only occur once metabolic demands have been satisfied. The remaining energy is then channelled to somatic or gonadal growth. Tuna are known to feed on a wide variety of prey (Sund et al 1981) and feed non-selectively based on local prey availability (Potier et al 2007). Evaluation of the stomach contents of tuna and other large pelagic species provides a snapshot of their diet while long-term feeding patterns can be studied through the analysis of stable isotopes such as $\delta^{15}N$ and $\delta^{13}C$. The feeding ecology of albacore tuna is investigated through examination of stomach contents coupled with analysis of stable carbon and nitrogen isotopes. A comparison of albacore tuna and yellowfin tuna (*T. albacares*)stable isotopes is made and the position of these two species within the food web of the southern Benguela region is estimated.

This study aims to investigate the morphometrics, growth rate, reproductive biology and diet of the albacore tuna of South Africa. The study is based on samples received from recreational fishermen. Morphometric and physiological parameters are compared with albacore tuna from other regions of the world. Diet comparison with yellowfin tuna, with which albacore are sympatric in South African waters, is also made. The repeatable nature of sampling tuna from angling competitions is a means of restarting a monitoring program that, if maintained, will create an invaluable database of biological data.

2.2 Materials and Methods

Albacore were sampled duringthreenational sport-fishing competitions in the Western Cape, South Africa,in May and October of 2012 and in May of 2013.The competitions were hosted by Simonstown Yacht Club, the Millers Point Boat and Ski Club and the Atlantic Boat Club in Hout Bay.Sampling took place on the 15th and 16th of May 2012, the 25th of November 2012 and on the 14th and 15th of May 2013. Fresh albacore (n=99) were processed on site and tissue material was bagged and frozen for later processing in the laboratory. Additional frozen fish (n=20)caught on the 5th of May 2012 were received from a commercial fisher. Due to time constraints and the availability of samples a different number of fish were used for various applications in this study (Table 2.1).

Table 2.1: Number of fish sampled from angling competitions and a commercial fisher, sex of the samples (M-male, F, female, ND, not determined/indeterminate) and the number of fish used in the different applications of this study.

Source		Sex			Morphometrics	Aging	Diet	Stable Isotope Analysis	
Competition	Commercial	M	F	ND				*T. alalunga*	*T. albacares*
99	20	65	39	15	119	51	62	47	16

2.2.1 Morphometrics

Whole fish were weighed on a hanging scale to the nearest 10 g or a desktop scale was used to weigh small fish to the nearest 1 g. Measurements of fork length (FL), first dorsal length (DL1), thorax girth (TG), body height (BH), the length from the posterior operculum margin to the caudal keel (OCKL), mouth height (Md), mouth width (Mw) and upper jaw length (UJL) were made using either callipers or a measuring tape (Figure 2.1).Measurements were made to the nearest mm.

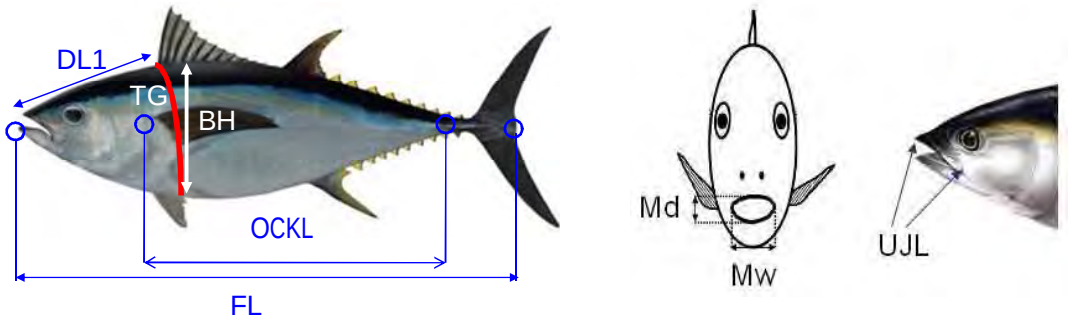

Figure 2.1:Morphometric measurements taken of albacore tuna (*Thunnus alalunga*).

For fresh specimensthe head was removed using a saw and stored on ice until transfer to a -20°C freezer in the laboratory. The first dorsal spine was cut-out carefully, so as not to snap the spine, and stored frozen. Fish were cut from the cloaca along the ventral cavity.Sex was determined by visual examination. Gonads were removed and weighed whole to the nearest 0.1 g. Maturity was estimated by visual examination on a scale used for examination of large pelagic fish gonads (Table 2.2).

Table 2.2: Maturity stages for visual examination of large pelagic fish gonads.

Stage	Criteria	
	Males	**Females**
	Juvenile gonads small ribbon-like, not possible todetermine sex by gross examination	
1	**Immature**: testes thin, flattened and ribbon-like, but sex determinable by gross examination	**Immature**: gonads elongated, slender, but sex determinable by gross examination
2	**Early maturing**: Testes enlarged but still immature, no milt in central canal	**Early maturing**: ovaries enlarged but individual ova not visible to the naked eye
3	**Maturing**: milt flows freely if testes pinched or pressed	**Late maturing**: ovaries enlarged, individual ova visible to the naked eye
4	**Ripe**: testes large, milt flows freely from testes	**Ripe**: ovary greatly enlarged, ova translucent, easily dislodged from follicles or loose in lumen of ovary
5	**Spent**: testes flabby, bloodshot, surface dull red, little or no milt in central canal	**Spawned**: includes recently spawned and post-spawning fish, mature ova remnants in various stages of resorption, and mature ova remnants about 1.0 mm in diameter

Ovaries were sectioned in four places at equal intervals along the ovary and sections were preserved in formalin. The stomach, intestines and vital organs were removed. A 2-4 cm^3

section of the liver was removed and stored in glass microcentrifuge tubes. This sample was re-cut and used for stable isotope and fatty acid analysis. A 2-4 cm^3 muscle sample was removed from the position just behind the head and in front of the dorsal spine. This sample was re-cut and stored in separate glass tubes for isotope, genetic or fatty acid analysis. The muscle and liver isotope samples were kept frozen at -20°C, the fatty acid samples stored at -80°C and the muscle genetic samples preserved in ethanol and stored at -80°C. The stomach was weighed to the nearest g and kept on ice before transfer to a -20°C freezer in the laboratory. Headed and gutted weight was measured after processing of the fish was complete.

A variety of morphometric measures were regressed against fork length using either linear or power functions. In some cases males and females were regressed separately and differences in slopes were tested using the t-test and Chi-squared contingency (Zar 2009).

Fulton's condition factor (K) was used to calculate the condition index

$$K = 100 * \frac{W}{FL^3} \quad , \qquad \text{Equation 1}$$

Where W is the whole body wet weight and FL is the fork length.

2.2.2 Aging

2.2.2.1 Otoliths

Whole sagittal otoliths were removed from fish skulls using metal forceps. Otoliths were cleaned, air-dried and then stored in dry, labelled, Eppendorf microcentrifuge tubes. The position of the nucleus was estimated and marked before otoliths were set in clear Polyester resin for sectioning. Sagittal otoliths embedded in resin were sectioned transversally on either side of the nucleus mark using a twin wafering-blade saw. Sections were cut between 0.2 and

0.3 mm thick. Sections were mounted on a cover slip and fixed to a microscope slide using DPX mountant. DPX mountant was placed between the microscope slides as well as on top of the section to increase clarity when viewing under a microscope.

Ring countswere performed using a stereomicroscope (Nikon SMZ1500) under transmitted light at 40X magnification and a photograph was taken using a 524 megapixel colour charged-coupled device camera linked to the microscope. Growth bands were identified as alternating narrow translucent zones and wider opaque zones (Figure 2.2). The marginal increment zone was noted as either opaque or hyaline for each otolith. The frequency of opaque deposition was compared between May and October samples. The size of the marginal growth zone will vary depending on the time of sampling during the year (Mendoza 2006). A pair consisting of a hyaline and opaque zone was assumed to be equivalent to the passing of one year. Age was estimated on three occasions as the count of opaque zones, by a single reader over a period of one year, with no reference to previous counts. The median count for each fish over the three reads was taken as the age of that fish. The age by counts of opaque rings was adjusted for time of year that fish were sampled.

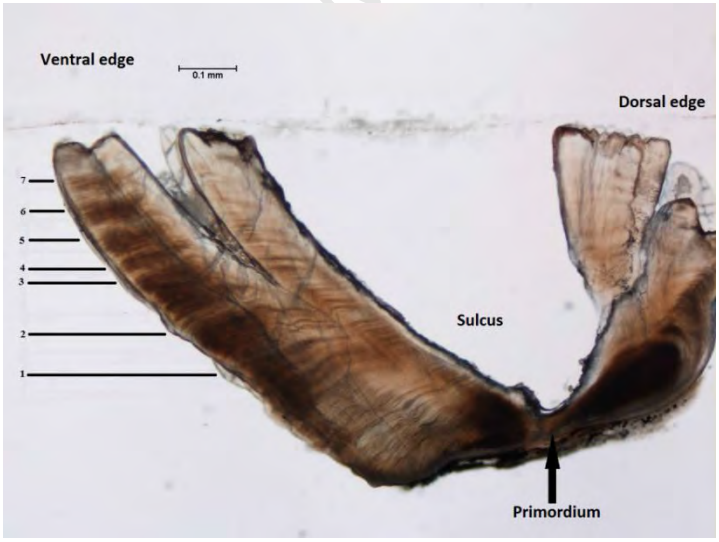

Figure 2.2: Transverse section of a left sagittal otolith from *Thunnus alalunga*. Growth increments were read along the ventral edge.

2.2.2.2 First Dorsal Spine

The methods used for spine processing were the same as those used by Cheng et al(2012). Spines were soaked in a hot water bath for 5-6minutes at 80-90°C until all attached muscle was flexible. Adhering muscle was removed and the spines cleaned before air-drying andstorage. The total length of the spine, L, was defined as the length from the base of the spine condoyle to the tip of the spine. The width of the spine condoyle was defined as length C (Figure 2.3). Measurements were made to the nearest 0.01mm using a digital vernier calliper. Spines were embedded in clear epoxy resin by the same process as used for otoliths. A cross-section was taken at lengths equal to half-C and C above the condoyle base using a twin wafering-blade saw. Sections ranged from 0.8-1.0mm thick. Sections were mounted on a glass slide using translucent DPX mountant and examined under a stereo microscope at 0.75-2X magnification. Images of dorsal spine sections were captured and analysed using NIS Elements Documentation and Digital 3D Imaging software. The morphological parameters of the spine section were measured at the same time as images were captured. The parameters included: the diameter of the spine (d) and the distance between ring*i* and the distal spine edge beyond ring *i* (d_i).The radius of the spine section (R) and the radius of the annual ring *i* (R_i) were then calculated: R=d/2, R_i=d_i-R (Fig. 2.3b). Growth bands were identified as alternating translucent and opaque zones. The age of each fish was estimated by counting the number of opaque zones.

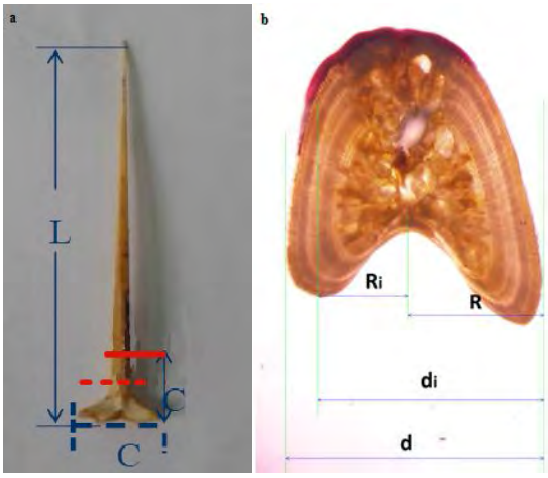

Figure 2.3: a) First dorsal spine showing the defined length of the spine, L, and the base of the spine, C, as well as the positions that a transverse section was taken, at length C above the condoyle base (solid line) and length 1/2C (dashed line). b) Measurement parameters of spine cross-section, R: radius of spine cross-section, d: diameter of spine cross-section, Ri: radius of ring *i*, di: distance between annual ring *i* and the distal spine edge beyond ring *i*.

2.2.2.3 Statistical Analysis

Precision of aging was measured as a means of determining the reproducibility of age determinations (Campana 2001). The average percentage error (APE)was calculated according to Beamish and Fournier (1981):

$$APE = 100\% \times \frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j} \quad , \qquad \text{Equation 2}$$

where*R* is the number of times each fish was aged, X_{ij} is the i^{th} age determination of the j^{th} fish and X_j is the average age estimate of the j^{th} fish.

When the absolute deviation from the mean age is substituted with the standard deviation from the mean age (Chang 1982) the coefficient of variation (CV) can be estimated. The coefficient of variation (CV) was calculated as:

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^{R}\frac{(X_{ij}-X_j)^2}{R-1}}}{X_j} \quad , \qquad \text{Equation 3}$$

where CV_j is the age precision estimate for the j^{th} fish.

2.2.2.4 Modelling fish growth

The von Bertalanffy growth function (VBGF) was used to model fish growth, as described by the equation, $L_t = L_\infty * (1 - e^{(-K*(t-t_0))})$, where L_t is the fork length at age t, L_∞ is the theoretical asymptotic fork length, K is the Brody growth coefficient, t is the age in years and t_0 is the theoretical age of a zero length fish. Of the 51 readable otoliths, two otoliths were excluded as there was no agreement between age estimates for those fish. The VBGF was

fitted to the remaining age and fork length data to obtain the growth parameters (L_∞, K and t_0) by least squares nonlinear regression to minimise the sum of squares.

The goodness of fit of the VBGF was evaluated by R^2 (Motulsky and Christopoulos 2004). The R^2 value can be calculated as $R^2 = 1 - (\frac{S_R}{S_T})$ where S_R is the residual sum of squares and S_T is the total sum of squares.

2.2.2.5 Intra-specific life history comparison

Existing age-derived life history parameters for *T. alalunga* populations across a range of locations were collated from available literature. For ease of contrast between this study and growth studies conducted on other populations of *T. alalunga*, the growth performance index (ϕ') was calculated:

$$\phi' = logK + 2\,logL_\infty \quad , \qquad \text{Equation 4}$$

where$\phi'$is measured in cm (Pauly 1978). This index was proposed to describe the interaction and dependence of the von Bertalanffy parameters L_∞ and K. It has been found that similar populations, species or families often have similar ϕ' estimates although their growth parameters may differ.

2.2.3 Feeding Ecology

The stomach contents of 62 fish were examined to analyse the diet of albacore tuna in South African waters. Muscle samples were taken from 47 albacore tuna and 17 yellowfin tuna during sampling at the fishing competitions for stable isotope analysis (SIA) to compare two similar pelagic tuna species.

2.2.3.1 Stomach Content Analysis

The level of repletion of each stomach was estimated on a scale of 1 (100%)to 4 (0%), to give an indication of the fullness of each stomach before analyses. Stomach contents can be separated into fresh or partly digested items and accumulated items such as indigestible hard part structures. All contents were removed and the lining was rinsed to dislodge any small material and gastric fluid. The total content mass was weighed to the nearest mg. Bait (cut sardine) was identified, weighed and discarded.

Fresh remains were sorted into broad groups (fish, crustaceans, cephalopods and other) and weighed to indicate the proportion of the diet each group represented by wet weight. The number of individuals was estimated for each group by counting the fresh remains.For fish the number of vertebral columns was counted.The number of telsons or whole individuals was recorded to count crustaceans. Cephalopod skin and suckers are rapidly digested, therefore the greatest number of upper or lower beaks and gladius were counted and beaks were used to determine species.For groups of individuals total wet weight was divided by the number of prey to calculate individual mass. Prey items were measured -standard length for fishes, gladius length and lower rostral length of lower beaks for cephalopods and total and telson length for crustaceans.

For accumulated items, otoliths were collected loose and the number of pairs was counted for fish and recorded. Loose cephalopod beaks were counted, sorted and removed from further analysis, as they can over-emphasise the importance of cephalopods in the diet.

Each prey item was allocated a digestion state using a key designed specifically for each group (Pusineri et al 2003). Individual prey items were identified to the lowest possible taxon using keys and descriptions from Monod(1968), Crosnier and Forest (1973), Clarke, Ed.(1986), Smith and Heemstra, Eds. (1991) and Smale et al(1995).

Three diet indices were calculated for each prey species and for each prey group. Percent Frequency of occurrence (%FO) is measured as the proportion non-empty stomachs within which the prey species or prey group was found. The mean proportion by number (%N) is the percentage that each prey species or group contributes to the total number of prey items, while the mean proportion by weight (%W) is the contribution to the total weight by each prey species or group. Prey-specific abundance, defined as the percent numerical abundance of a prey item averaged over the stomachs in which it occurs, was calculated according to Brown et al (2012). Consequently a prey-specific index of relative importance (PSIRI) could be determined.This is shown by Brown et al (2012) to be stronger than the traditional index of relative importance (IRI). PSIRI is comparable between studies when different criteria and methods are used for diet analysis.

2.2.3.2 Stable Isotope Analysis

Stable Isotope Analysis (SIA) was performed for both albacore and yellowfin tuna. SIA was performed twice on each sample, once at the University of Cape Town (UCT) and once at La Rochelle, France.

At UCT samples were soaked in de-ionized water for 3 hours to remove excess salt before freeze-drying overnight at -40°C (Edwards Freeze-Dryer Modulyo).Neither freezing nor freeze-drying affects $\delta^{13}C$ or $\delta^{15}N$ signatures (Bosley and Wainright, 1999). Dried material was halved, half for analysis at UCT, half for analysis at La Rochelle. Defatting of the muscle tissue is required as lipids are rich in carbon. The amount of fat reserves in an individual fish varies depending on season, sex and size. It is therefore preferable to remove lipids so as to only take into account the elements that remain stable.

At UCT dried material was immersed in a buffer of methanol, chloroform and de-ionized water in theratio 2:1:0.8 for forty five minutes to remove lipids. Samples were again freeze-

dried overnight. Between 0.4 and 0.6mg of the dried material of each sample was weighed in tin cups to an accuracy of 1 µg on a Sartorius micro balance. The cups were mechanically squashed to enclose the sample. The samples were combusted in a Flash 2000 organic elemental analyser and the gases passed to a Delta V Plus isotope ratio mass spectrometer (IRMS) via a Conflo IV gas control unit (Thermo Scientific, Bremen, Germany). The standards used were valine (Sigma), MG (Merck Gel) and Seal (a seal bone crushed, demineralized and dissolved in acid, and then reconstituted in gel form at UCT). All the standards were calibrated against IAEA (International Atomic Energy Agency) standards, either by UCT or by other labs. Nitrogen is expressed in terms of its value relative to atmospheric nitrogen, while carbon is expressed in terms of its value relative to Pee-Dee Belemnite.

In France samples, received from UCT, were prepared by Jean-Baptiste Tissot at the Institut de Recherche pour le Développement (*IRD*), *Sète*. They were first frozen to remove any excess water in the tissue using a Christ Alpha 1-4 freeze dryer for 72 hours. Dried, frozen samples were then ground into a fine, dry, homogenous powder using the automatic ball mill Retsch MM200.

The lipid reserves were removed by an automated Accelerated Solvent Extractor (Dionex ASE 200) using the non-polar solvent dichloromethane (CH_2CL_2) combined with an increase in temperature and pressure. The delipidated samples were then stored in separate cryotubes.

The amount of lipid in each sample was calculated by weighing the tubes containing both extracted lipids and solvent, then evaporating out the solvent using the RapidVap at 40 °C under a pressure of 250 mbar for 40 minutes, then reweighing the tube to determine the total weight of lipids. The lipid ratio could then be calculated as the percentage weight of the lipids in the original sample.

A certain mass of each delipidated sample was then weighed into tin capsules using a precision balance METTLER-TOLEDO XP6 Model. The capsules were mechanically squashed to enclose the sample.

Isotopic analysis by mass spectrometry was carried out in La Rochelle by combustion in an elemental analyser before separation of CO_2 and N_2 gas by gas chromatography and a mass spectrometer. Isotopic ratios were then determined by comparison with a reference gas set (information unavailable from La Rochelle).

The major difference in Stable Isotope Analysis between the two laboratories is at the phase of defatting.

2.3 Results

2.3.1 Morphometrics

A total of 119albacore ranging from 580–1140 mm (FL) were sampled during 2012 and 2013 off the Cape coast of South Africa.60% of the fish ranged from 75-94 cm (Figure. 2.4). 10% were smaller than 750 mm and 30% exceeded 950 mm. The sample included39 females, 65 males and 2small fishwhose sex was indeterminate. For 13 of the fish sex was not determined due to time constraints during sampling.

Based on the maturity stage scale for large pelagic fish gonads, 33 males were categorized as immature and 32 as early maturing. Seven females were graded as immature and the remaining 32 were early maturing. No late maturing, ripe or spent/spawned testes or ovaries were found in albacore from South African waters.

Assumptions of normality were met, both the t-test (mean female FL (mm) = 881.77, mean male FL (mm) = 873.22, t = 0.37, p <0.01) and a 10 (size categories) X 2 (sexes) chi-square contingency table test (Chi square = 16.01, df = 9, p = 0.06) suggest that there is no difference between male and female lengths and that there is an equal distribution of sexes across the size spectrum.

The relationship between total mass (g) and fork length (mm) was described by a power curve (Fig. 2.5). The best-fit length-weight relationship for both sexes combined was:

$$\boldsymbol{M\,(g) = 0.0000184\,FL\,(mm)^{3.008}} \qquad \textbf{(n =119, } \boldsymbol{R^2} \textbf{ = 0.97. p<0.001)} \qquad \text{Equation 5}$$

Length versus mass was plotted and regressed separately for male (r^2 = 0.98, p<0.001) and female (r^2 = 0.96, p<0.001) fish and a significant difference in slopes was calculated (t = 2.38,df = 100, p = 0.019). Male growth is isometric (growth exponent = 2.99, lower 95% =

2.87, upper 95% = 3.10). Female growth is hyper-allometric (growth exponent = 3.28, lower 95% = 3.05, upper 95% = 3.49).

The best fit length-weight relationship for males and females respectively was:

$$\boldsymbol{M\,(g) = 0.0000207\,FL\,(mm)^{2.991}}$$ **(n = 65, R^2 = 0.98, p<0.001)** Equation 6

$$\boldsymbol{M\,(g) = 0.00000297\,FL\,(mm)^{3.275}}$$ **(n = 39, R^2 = 0.96. p<0.001)** Equation 7

First dorsal length (mm), thorax girth (mm), body height (mm) and the length from the posterior operculum margin to the caudal keel (mm) were each related to fork length (mm) (Table 2.3). The tightest relationships were between first dorsal length (mm)and fork length (mm) (Figure. 2.6) and the length from the posterior operculum margin to the caudal keel (mm) and fork length (mm) (Figure. 2.7).

DL1 = FL x 0.3308 **FL = DL1 x 3.023** (n = 119, r^2 = 0.91, p<0.001) Equation 8

OCKL = FL x 0.5882 **FL = OCKL x 1.7** (n = 62, r^2 = 0.95, p<0.001) Equation 9

Table 2.3: Regression statistics for first dorsal length (DL1), thorax girth (TG), body height (BH) and the length from the posterior operculum margin to the caudal keel (OCKL) related to fork length (FL), (n – sample size, a – x variable, b – y-intercept).

Dependent	Independent	n	a	b	r^2	p
DL1 (mm)	FL (mm)	119	0.2904	34.713	0.91	p<0.001
TG (mm)	FL (mm)	119	0.627	38.056	0.88	p<0.001
BH (mm)	FL (mm)	119	0.23	16.2	0.82	p<0.001
OCKL (mm)	FL (mm)	62	0.599	-8.759	0.95	p<0.001

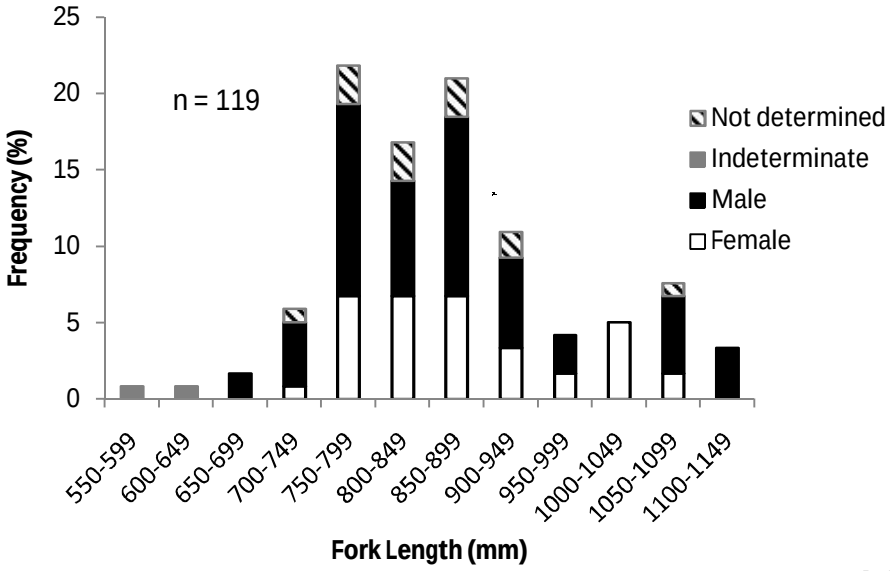

Figure 2.4: Size distribution of albacore tuna (*Thunnus alalunga*) sampled during 2012 and 2013.

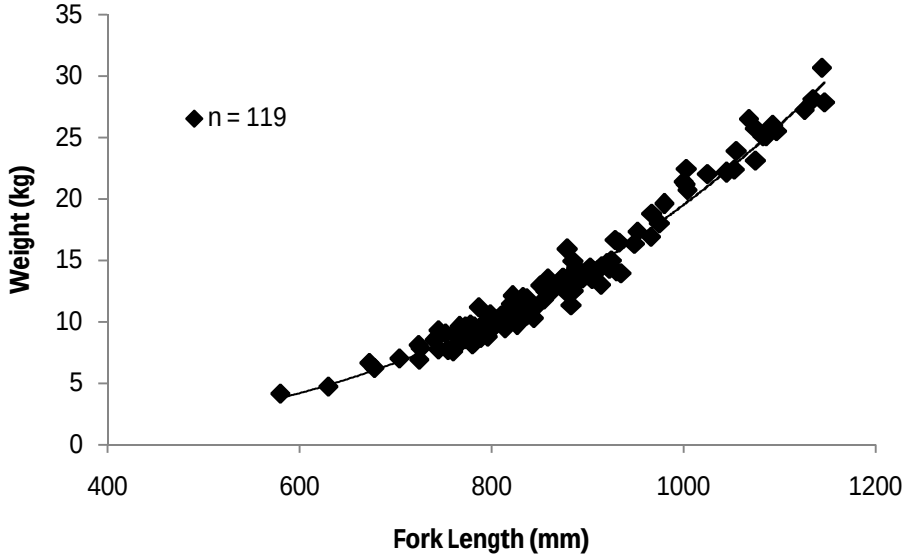

Figure 2.5: Scatter Plot of total mass (kg) against fork length (mm) for albacore tuna (*Thunnus alalunga*).

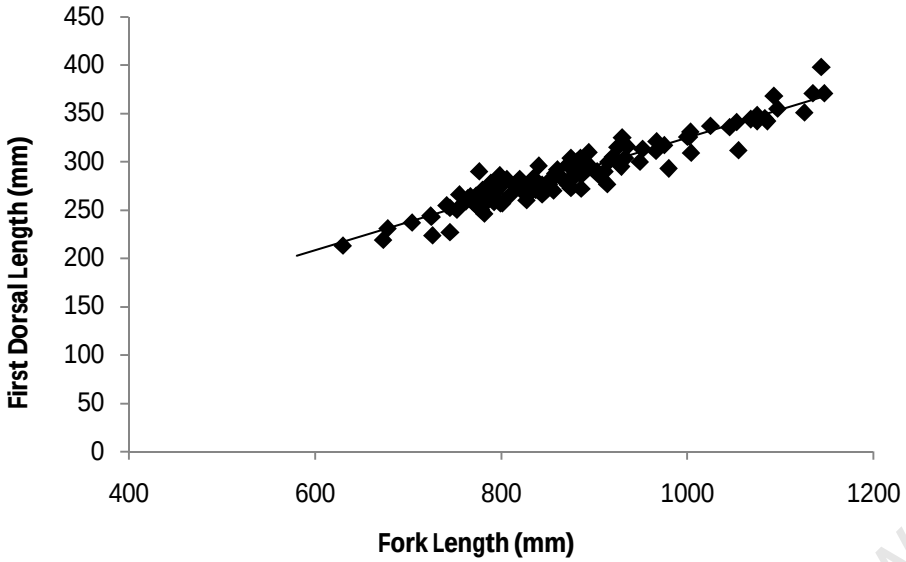

Figure 2.6: Scatter plot of first dorsal length (mm) against fork length (mm) for albacore tuna (*Thunnus alalunga*).

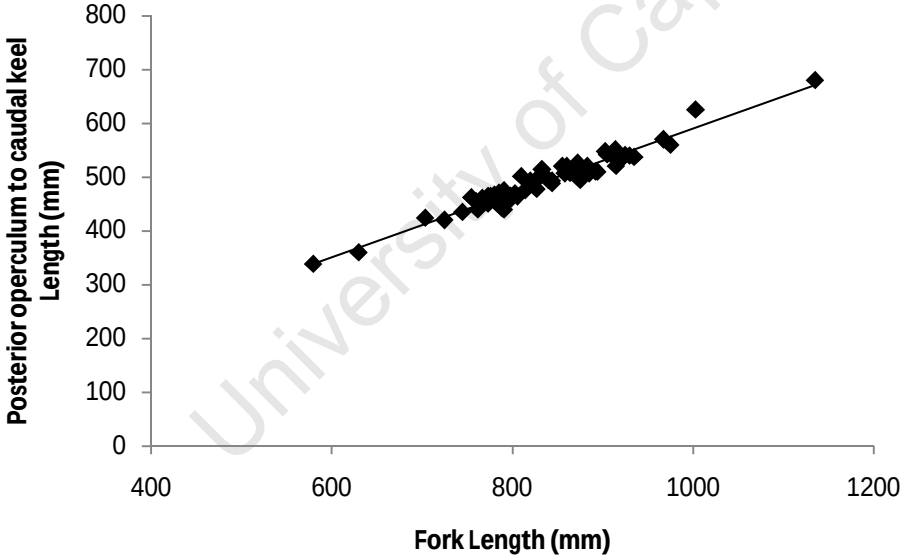

Figure 2.7: Scatter plot of posterior operculum to caudal keel length (mm) against fork length (mm) for albacore tuna (*Thunnus alalunga*).

Condition index (CI) was measured for each fish individually before a comparison was made between sexes, between seasons(May and October) for sexes combined and for each sex separately. There was a no significant difference between males and females (t=1.19, df=71, p=0.236). A significant difference was seen between May and October when sexes were

combined (t=3.27, df=20, p<0.05). No significant difference was seen between seasons for females(t=1.57, df=8, p=0.15). For males there was a significant difference between seasons (t=2.97, df=10, p<0.05).

2.3.2 Growth

A total of 51 fish (sampled in 2012), ranging from 58–114 cm (FL),yielded readable otoliths that were used to estimate von Bertalanffy growth parameters. Of the 51 otoliths aged, any two of the consecutive counts of growth zones were in agreement for 26 fish (51%) and all three counts agreed for 23 fish (45%) (Figure.2.8). Up to eight growth rings were visible in the otoliths. Average percent error (APE) was calculated for each fish and then averaged for all the fish to provide an index of APE of 7.99%. The CV was estimated for each fish separately then averaged across the sample to estimate a CV of 10.48%.

Twenty eight spines were prepared for age estimation. Spines were more difficult to read than otoliths (APE = 20.82%, CV = 28.67%) and the small sample size lead to spines being excluded from any further analysis of age.

A hypothetical birth date of January was assigned to albacore. Austral winter occurs roughly from June to October and summer from the end of October to May. Opaque zones are deposited during periods of slow growth, associated with winter. Hyaline growth zones are laid down during rapid growth that can be associated with summer. There was a higher prevalence of the marginal ring being opaque for fish caught in October than for fish caught in May. A 2 (ring type) X 2 (month) chi-square contingency table test (Chi square = 2.28, df = 1, p = 0.13) suggested that this difference is not significant.

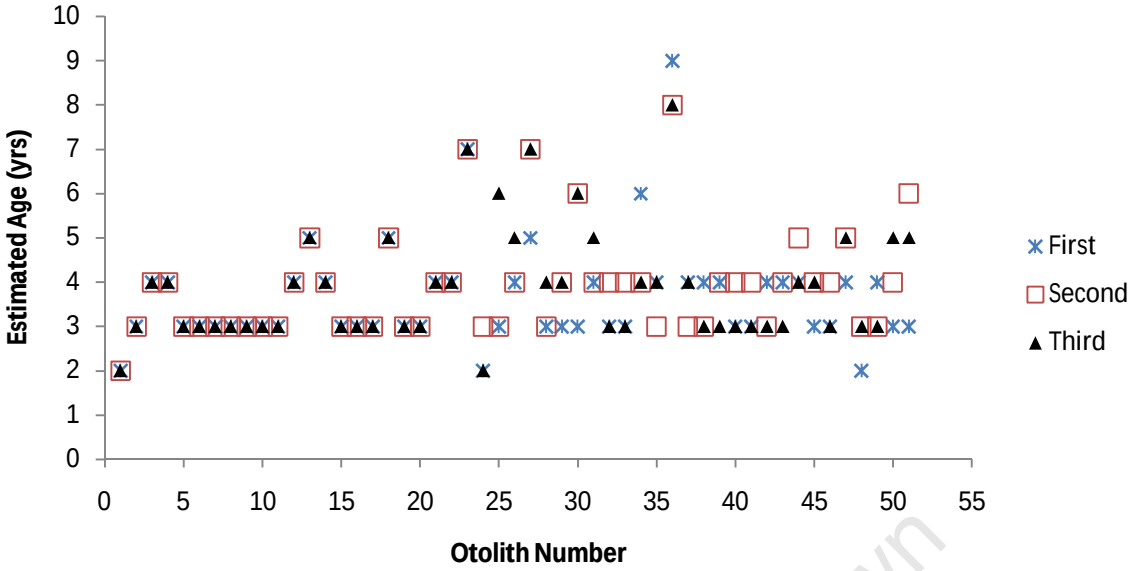

Figure 2.8: Age estimates for three consecutive counts made by a single reader in order from most to least repeatable.

Laurs et al (1985) calibrated the rate of increment deposition on sagittae of north Pacific albacore. They concluded that increment formation is a daily event, with an average of 0.954 increments formed for every day at liberty. Assuming a January birth date, aging by counting the number of opaque zones underestimated the age of fish sampled in May that had a large hyaline marginal zone. If it is assumed that hyaline ring deposition begins in October then the May fish would have grown for an additional seven months over the age estimated from opaque ring counts. Conversely fish caught in May that had already started depositing an opaque ring would have been over-aged by five months. Thus the median age from the three consecutive estimates was adjusted for these fish. The age estimated from opaque ring counts was not adjusted for fish caught in October, where the marginal zone was hyaline it was presumed that those fish had just recently completed opaque ring deposition.

The best-fit von Bertalanffy growth curve (Figure 2.9) and equation for the adjusted age estimates was:

$$\boldsymbol{FL\ (mm) = 1100.07 * \left(1 - e^{-0.238*(t-(-2.14))}\right)} \qquad \text{Equation 10}$$

The growth performance index was calculated at $\phi' = 3.46$ and is in the middle of the range of ϕ' calculated for other albacore stocks (Table 2.4).

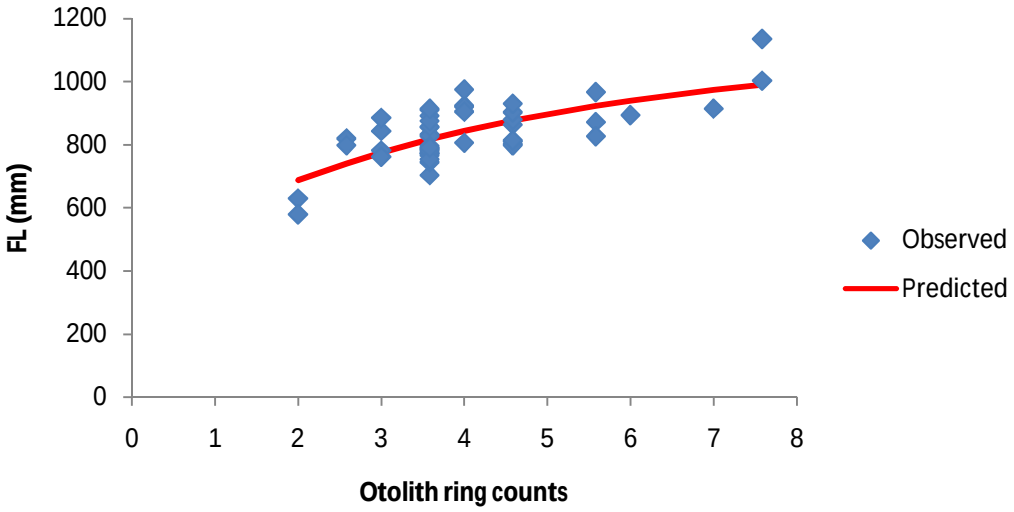

Figure 2.9: Estimated von Bertalanffy growth curve for southern Atlantic albacore tuna (*Thunnus alalunga*) obtained by non-linear fitting of Fork Length vs. otolith ring counts.

Table 2.4: Growth performance index for *Thunnus alalunga* from various stocks and localities, $\phi' = logK + 2logL_\infty$

Author	Stock	Region	ϕ'
Talbot and Penrith (1963)	South Atlantic	South Africa	3.43
van der Elst (1981)	South Atlantic	South Africa	3.46
Bard (1981)	North Atlantic		3.55
Lee and Liu (1992)	Indian Ocean		3.48
Lee and Yeh (1993)	South Atlantic	Northwest	3.47
Megalofonou (2000)	Mediterranean	Agean and Ionian Sea	3.36
Santiago & Arrizabalaga (2005)	North Atlantic	Bay of Biscay	3.47
Lee and Yeh (2007)	South Atlantic	Northwest	3.44
Cheng et al (2012)	Indian Ocean	Southern	3.40
Current study (2012)	**South Atlantic**	**South Africa**	**3.46**

2.3.3 Feeding Ecology

Stable isotope analysis (SIA) of $\delta^{15}N$ and $\delta^{13}C$ provides a more long-term measure of an organisms' relative trophic level than stomach content analysis. The latter provides only an instantaneous view of where an organism sits in the food web based on the prey items identifiable in the stomach. Differential digestion rates of prey species can lead to bias when examining stomach contents of upper trophic level species (Post 2002) as larger organisms such as fish, and crustaceans with chitinous carapaces, tend to be digested slower than smaller, lower trophic level species (Jobling 1987). Isotopes on the other hand are assimilated into an organism from metabolic and anabolic processes (Post 2002) and hence provide the ability to measure the time-integrated position of an organism in the food web. Tuna are pelagic predators and opportunistic feeders. They sample a wide range of small and large prey most likely from various baseline carbon sources. An integrated approach of analysing stomach contents and SIA therefore supports a better definition of such a species' trophic level.

2.3.3.1 Stomach Content Analysis

Stomach content analysis was carried out on fish ranging in size from 600 mm – 1050 mm fork length (Figure 2.10). Of the 62 stomachs sampled 10 contained only bait fish, 20 only prey matter, 27 contained both bait and prey and 5 were empty. Stomachs that were empty or contained only bait were not considered for the remainder of the analysis. Filling Index (%) was calculated as the ratio between the content mass of non-empty stomachs and the measured total mass of each individual, less the full-stomach mass. A Filling Index (FI) of >10% was found for 40% of the stomachs sampled but this included the weight of bait fish found in non-empty stomachs. Figure 2.11 indicates a much lower FI when only the prey weight is considered in the calculation.

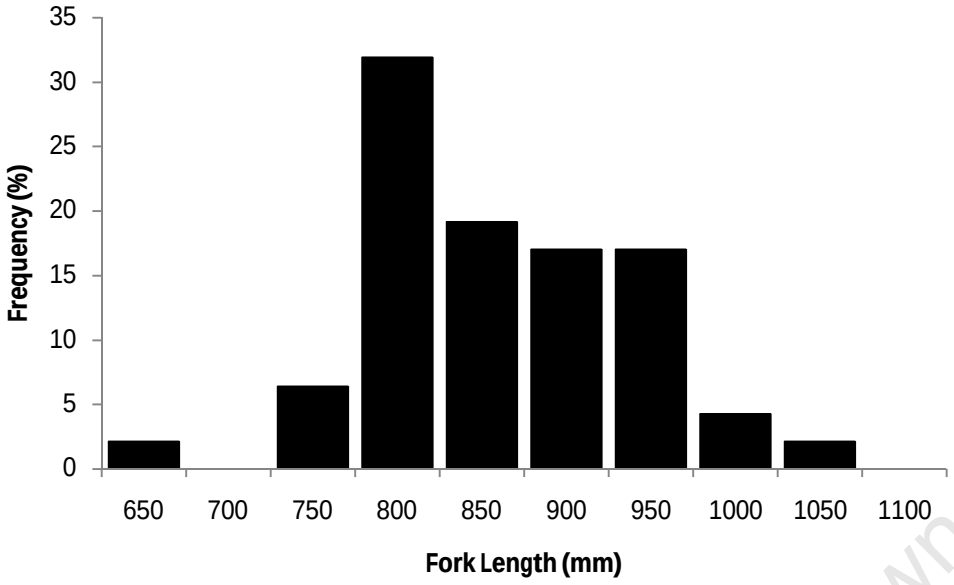

Figure 2.10: Size distribution of *T. alalunga* for which stomach contents were analysed.

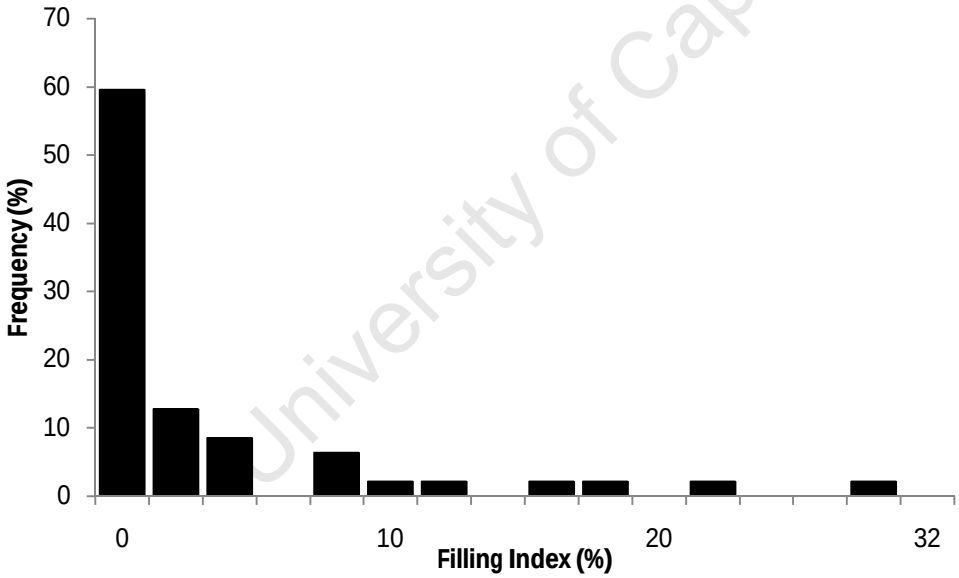

Figure 2.11: Filling Index (%) distribution for non-empty fish stomachs (Prey weight only).

Of the 47 stomachs that contained prey only or both bait and prey, a total of 294 prey items were identified (Table 2.5). Of these 77 were fish that belonged to seven species and five families, 53 cephalopods of the same species, and 164 crustaceans corresponding to three families and three species as well as larvae of various species.

Based on absolute measures of abundance it can be seen that crustaceans accounted for >50% of the prey items by number but <6% by weight. The most common prey items were shrimp larvae(59), not further identifiable due to the degree which they had been digested. The hyperiid amphipod *Brachyscelus crusculum* was the next most important crustacean by number (54) followed by lobster larvae (40). Fish species contributed 26% by number and 44% by weight. Of the identified fish species *Maurolicus muelleri* was the most important by number (56) but it was the two whole individuals of deep-water hake (*Merluccius capensis*) that contributed most by weight, 182 g. Cephalopods accounted for only 18% of prey items by number but 50% by weight, the only species identified, by examination of beak morphology, was *Lycoteuthis lorigera*, that occurred in 24 stomachs.

Prey-specific measures of abundance are calculated by considering only the stomachs in which a prey item occurs (i.e. by ignoring zero values for stomachs not containing that prey species or group). Crustaceans were once again dominant by number accounting for 74% of the prey items in the stomachs in which they occurred, fish and crustaceans made up 61% and 69% of the prey items in the stomachs they were found in respectively. In stomachs where fish occurred 82% of the weight was attributable to this group, while when cephalopods were present they contributed 75% by weight. According to the %PSIRI crustaceans were the most important prey group for albacore, this owing to their high occurrence (27) and absolute numbers (164). Although crustaceans did not contribute a significant weight in the stomachs where they were found, of the 47 stomachs examined 14 contained only crustaceans, as a result of this the prey-specific weight for this group was 55.5% and consequently PSIRI was 37.15%. Cephalopods contributed 36.92% of the PSIRI.Although they had the lowest absolute numbers (53) they were the most important group by weight. According to a PSIRI of 25.93%, fish were the least important prey group for albacore.

2.3.3.2 Stable Isotope Analysis

There was a significant difference between the stable isotope values for *T. alalunga* processed at UCT and La Rochelle ($\delta^{13}C$, t = -4.58, df = 46, $p<0.05$; $\delta^{15}N$, t = -6.84, df = 46, $p<0.05$) as well as for *T. albacares* ($\delta^{13}C$, t = -4.53, df = 15, $p<0.05$; $\delta^{15}N$, t = -2.57, df =15, $p<0.05$) (Table 2.6). The results obtained from the University of La Rochelle were used for further analysis because the defatting stage described in the materials and methods (2.2.3.2) was performed more effectively, as seen by the high average C:N ratios for fish muscle samples processed at UCT (*T. alalunga* = 3.62, *T. albacares* = 3.78) compared with the average C:N ratios from La Rochelle (*T. alalunga* = 3.14, *T. albacares* = 3.11).

Table 2.6: Mean ± standard deviation and (range) $\delta^{13}C$ and $\delta^{15}N$ stable isotope values for forty seven albacore tuna (*T. alalunga*) and sixteen yellowfin tuna (*T. albacares*). Stable Isotope Analysis was performed twice per tissue sample, at UCT and La Rochelle Universities.

		UCT		La Rochelle	
Species	N	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
T. alalunga	47	-17.70±0.88 (-16.42/-20.29)	13.60±0.70 (11.58-14.97)	-17.16±0.39 (-17.9/-16.06)	13.92±0.62 (12.6-15.07)
T. albacares	16	-17.30±0.79 (-18.52/-16.21)	13.63±0.61 (12.33-14.90)	-16.56±0.26 (-16.87/-15.99)	13.78±0.58 (12.96-15.24)

$\delta^{13}C$ is significantly different between albacore and yellowfin (t-test unequal variance, t = 2.02, $p<0.001$) (Figure 2.12). Regardless of the size of the fish sampled both species share the same range of $\delta^{15}N$ stable isotope values (t-test unequal variance, t = 2.05, p = 0.42) (Figure 2.13). Analysis of similarities (ANOSIM) was performed in Primer V6, in Bray-Curtis distance, and showed that there is a significant difference between the two species combined $\delta^{13}C$ and $\delta^{15}N$ stable isotope values (R = 0.194, p = 0.005) (Figure 2.14).

Table 2.5: Occurrence (O) and Frequency of occurrence (%FO), absolute number (Nabs) and wet weight (Wabs), percentage contribution by number (%N) and weight (%W), mean proportion by number (%MN) and mean proportion by wet weight (%MW), prey specific contribution by number (%PN) and prey specific contribution by weight (%PW) and prey specific index of relative importance (%PSIRI) of prey species or categories recovered from stomach contents (47 samples) (*Thunnus alalunga*).

Prey family	Prey species	O	%FO	N_{abs}	%N	MN%	%PN	W_{abs}	%W	MW%	%PW	%PSIRI
Fish		**17**	**36.2**	**77**	**26.2**	**22.20±36.96**	**61.4**	**857.1**	**43.7**	**29.66±43.25**	**82.0**	**25.93**
Myctophidae	*Diaphusspp.*	1	2.1	2	0.7	0.25±1.72	11.8	10.6	0.5	1.61±11.01	75.5	0.93
Paralepididae	*Lestidiops similis*	4	8.5	5	1.7	5.32±18.75	62.5	46.3	2.4	7.06±23.96	82.9	6.19
Sternoptychidae	*Maurolicus muelleri*	2	4.3	56	19.0	4.21±20.18	98.9	102.4	5.2	4.25±20.39	99.9	4.23
Merlucciidae	*Merluccius capensis*	2	4.3	2	0.7	3.19±16.17	75.0	182.3	9.3	3.86±18.62	90.8	3.53
Scorpaenidae	*Helicolenus dactylopterus*	1	2.1	1	0.3	1.06±7.29	50.0	173.0	8.8	1.80±12.36	84.8	1.43
	Engraulis capensis	1	2.1	1	0.3	0.16±1.12	7.7	75.8	3.9	0.62±4.27	29.2	0.39
	Sardinops ocellatus	1	2.1	1	0.3	0.06±0.38	2.6	60.5	3.1	1.94±13.30	91.2	1.00
	Fish larvae	3	6.4	4	1.4	2.42±14.64	37.9	0.5	0.0	2.14±14.59	33.5	2.28
	Unknown fish	3	6.4	5	1.7	5.53±21.95	86.7	205.7	10.5	6.37±24.67	99.9	5.95
Crustacea		**27**	**57.4**	**164**	**55.8**	**42.44±43.72**	**73.9**	**111.1**	**5.7**	**31.86±45.36**	**55.5**	**37.15**

Penaidae	*Penaidea*	2	4.3	2	0.7	1.23±7.35	28.8	30.3	1.5	1.01±6.32	23.8	1.12
Caridae	*Plesionikaspp*.	1	2.1	1	0.3	2.13±14.59	100.0	1.0	0.1	2.13±14.59	100.0	2.13
Brachyscelidae	*Brachyscelus crusculum*	17	36.2	54	18.4	21.65±33.72	59.8	11.9	0.6	11.67±30.90	32.3	16.66
	Stomatopod larvae	1	2.1	1	0.3	1.06±7.29	50.0	0.3	0.0	0.04±0.26	1.8	0.55
	Shrimp larvae	5	10.6	59	20.1	5.47±20.77	51.4	3.3	0.2	4.21±19.94	39.6	4.84
	Lobster larvae	8	17.0	40	13.6	9.99±26.49	58.7	40.2	2.0	12.51±33.02	73.5	11.25
	Crab larvae	2	4.3	2	0.7	0.10±0.49	2.4	0.2	0.0	0.10±0.66	2.3	0.10
	Unknown crustaceans	1	2.1	5	1.7	0.82±5.61	38.5	24.0	1.2	0.20±1.35	9.3	0.51
Cephalopods		**24**	**51.1**	**53**	**18.0**	**35.35±40.83**	**69.2**	**995.0**	**50.7**	**38.48±45.53**	**75.4**	**36.92**
Lycoteuthidae	*Lycoteuthis lorigera*	24	51.1	53	18.0	35.35±40.83	69.2	995.0	50.7	38.48±45.53	75.4	36.92
		47		**294**	**100.0**			**1963.2**	**100.0**			**100.00**

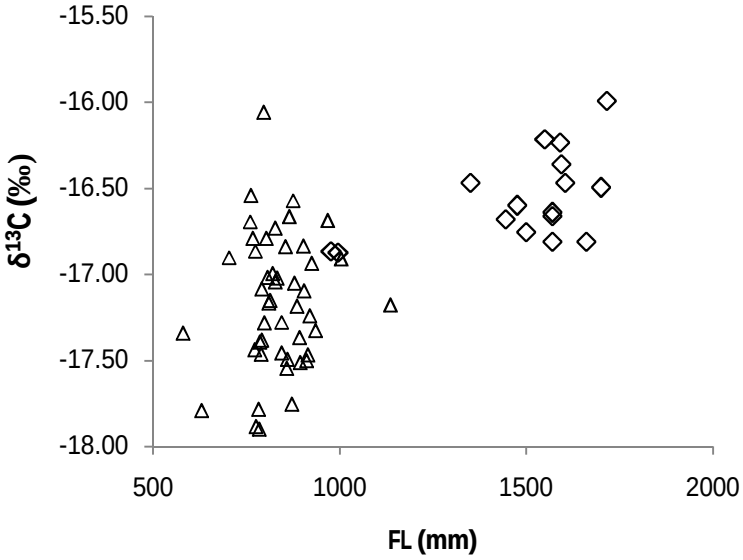

Figure 2.12: $\delta^{13}C$ stable isotope values for albacore tuna (*Thunnus alalunga*) and yellowfin tuna (*Thunnus albacares*) muscle samples plotted against fork length (mm). Δ - *T. alalunga,* ◊ - *T. albacares* processed at La Rochelle.

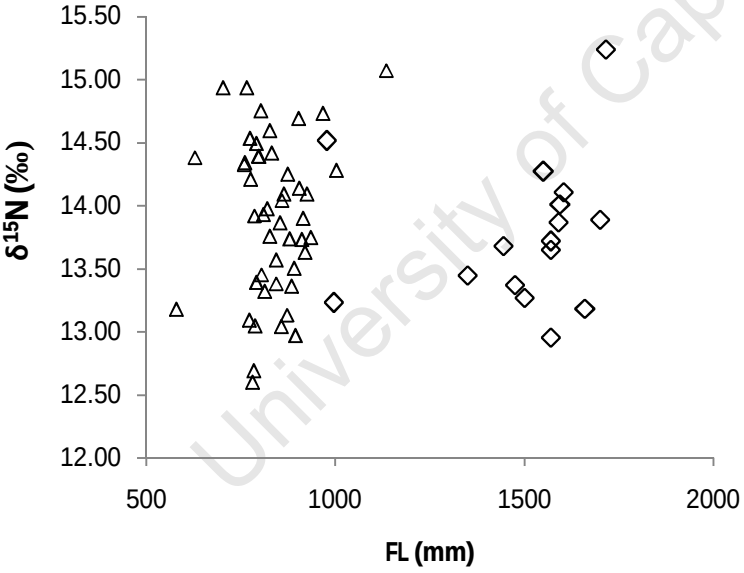

Figure 2.13: $\delta^{13}C$ and $\delta^{15}N$ stable isotope values in the muscles of albacore tuna (*Thunnus alalunga*) and yellowfin tuna (*Thunnus albacares*) processed at La Rochelle. Δ - *T. alalunga,* ◊ - *T. albacares* processed at La Rochelle.

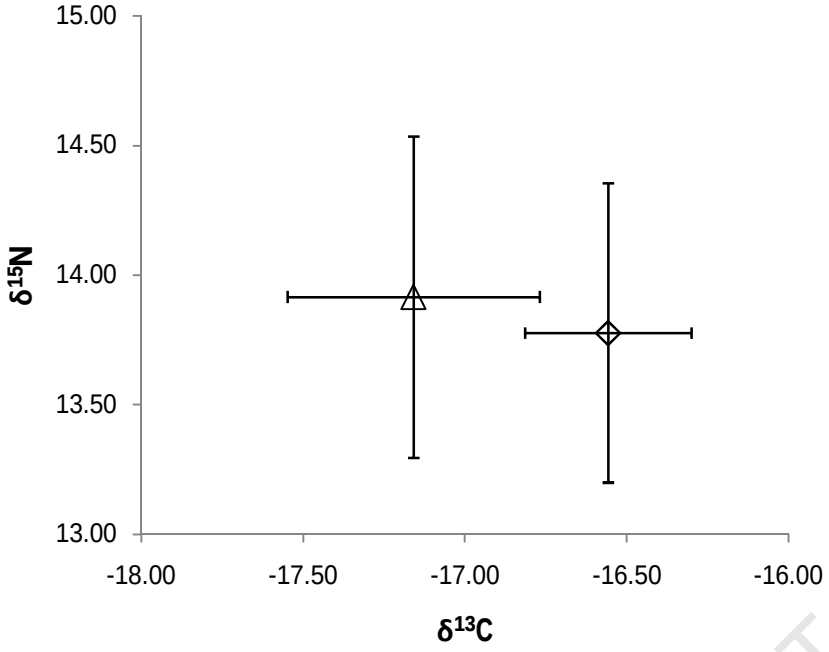

Figure 2.14: Meanδ^{13}C and δ^{15}N stable isotope values in the muscles of albacore tuna, *Thunnus alalunga*(Δ)and yellowfin tuna, *Thunnus albacares*(◊) (error bars indicate one standard deviation from the mean).

2.4 Discussion

2.4.1 Review of current study

This study focused on the age and growth, and feeding ecology of albacore tuna caught in South African waters in the region of Cape Point. Apart from fish received from a commercial fisher all the fish sampled were caught during angling competitions that focused ontargeting the larger yellowfin tuna (*Thunnus albacares*). Anglers target larger fish during competition so very few albacore below 70 cm could be included in the study. Angling contests do however provide a very useful platform for the study of tuna and tuna-like species. Newcombe (2011), in his study of the tuna sports fishery along the coast of South Africa, recognised that greater coverage and sampling at fishing contests would provide a wide range of individuals, juveniles, sub-adults and adults, as well as a broad coverage of the habitiat range for tuna and tuna-like species. Additional sampling from alternate gear such as longlines would be required to encompass the full size range of tuna. The South African baitboat fleet has an average catch-at-size of 82 cm FL, catches range from 42 – 114 cm (Alonso et al 2005) indicating that fish of smaller size do occur in South African waters.

2.4.2 Morphometrics

The predicted weights of South African albacore across the size spectrum are lower than those predicted for north Atlantic (Santiago 1993) and south Atlantic (Penney 1994) albacore but higher than those predicted for Indian (Hsu 1999) and Mediterranean (Megalofonou 1991) albacore (Figure 2.15). The range of predicted weights at 90 cm for these studies is 13.25 – 15.77 kg. At 90 cm (the mean length of albacore sampled in this study was 87 cm) the current work predictsa weight of 13.91 kg, central among the predictions for albacore stocks. Factors that may affect the estimation of length and weight coefficients include the

sampling of different stocks, sex ratio, thecondition of fish and storage conditions (Chen et al 2012).

It has been proposed that mixing of south Atlantic and Indian Ocean albacore stocks occurs in the region south of Africa (Koto 1969, Morita 1978, Fonteneau 2004) thus it is possible that the fish in this study were of either Indian or south Atlantic origin. This may explain why the length-weight relationship from the current study was intermediate between those of Penney (1994) and Hsu (1999).

Of the 119 albacore sampled 80% were weighed fresh, within a couple hours of being landed, the remaining 20% were thawed from frozen before weighing. The fresh quality of the fish provides confidence in accurate weight measurements. Fish that were thawed weighed on average 0.49 kg less than their respective predicted weights.

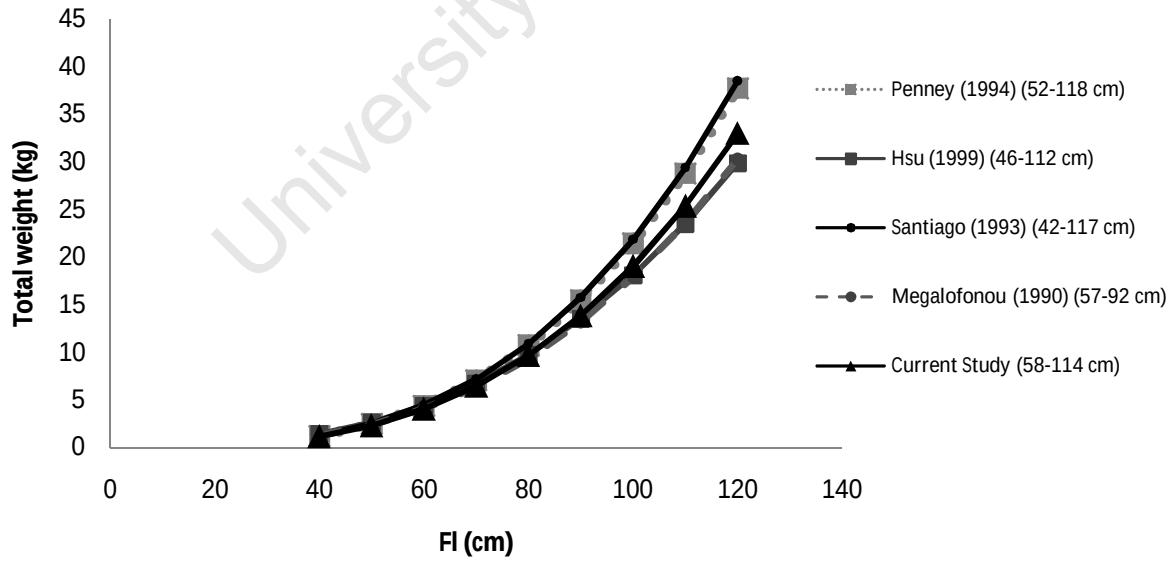

Figure 2.15: Length:weight relationship for albacore tuna (*Thunnus alalunga*) from the north Atlantic (Santiago 1993), the south Atlantic (Penney 1994), the Mediterranean Sea (Megalofonou 1991), the Indian Ocean (Hsu 1999) and the south Atlantic (Cape Point region, current study).

The sex ratio in this study, females:males, was 1:1.7. The deviation of the sex ratio from 1:1 would have an effect on the predicted length and weight coefficients as it was shown that male growth is isometric while female growth is hyper-allometric. Most likely females require a greater volume for ovaries after sexual maturation. 22 of the 39 females were greater than 85 cm fork length. Albacore are predicted to be sexually mature from 85 to 90 cm (Otsu and Hansen 1962, Bard 1981). For fish somatic and gonadal growth are seen to be in competition and it is common to see a decrease in somatic growth during maturation (Jobling 1994). 32 of the 39 females sampled in this study were categorised as "early maturing" by visual examination of their ovaries. The differences in growth seen for males and females in this study could be related to females going through maturation.

According to Penney (1994) the condition index (CI) of albacore from the south Atlantic is lowest in May.There was no significant difference seen between seasons for females in this study. For males there was a significant difference in CI between seasons.Further investigation of seasonal variation by exploration of condition factors indicated that the monthly change in condition is slight and probably insignificant for albacore caught in the commercial baitboat fishery (Penney 1994).

2.4.4 Growth

A variety of structures including spines (Bard 1981, Lee and Yeh 1993, 2007; Megalofonou 2000, Cheng et al 2012), otoliths (Laurs et al 1985, Chen et al 2012), scales (Haung et al 1990) and vertebrae (Lee and Liu 1992) have been used to age albacore tuna (*Thunnus alalunga*). In this study a comparison was made between the use of first dorsal spines and sectioned sagittal otoliths for aging albacore tuna. Based on the precision of aging, otoliths provided more precise age estimates. It was quicker to acquire spines during sampling but

preparation of this hard part structure was more laborious than preparation of otoliths. The extraction of otoliths was done in the laboratory the day after sampling and thus did not effect the number of fish sampled on site. Spines were rejected from further age analysis due to the difficulty in repeatedly estimating the same age from each sample. It is the opinion of this researcher that identification of annuli for estimating age of albacore tuna was easier using sectioned otoliths than using first dorsal spine sections.

The von Bertalanffy growth parameters predicted for *T. alalunga* from this studydiffer from those currently used by ICCAT. There are differences in growth rate and maximum length for albacore tuna between this study and other work (Figure 2.16).A comparison of the growth performance index (ϕ') however shows that the value of 3.46 calculated in this study is central among the ϕ'values reported for previous studies (Table 2.4).

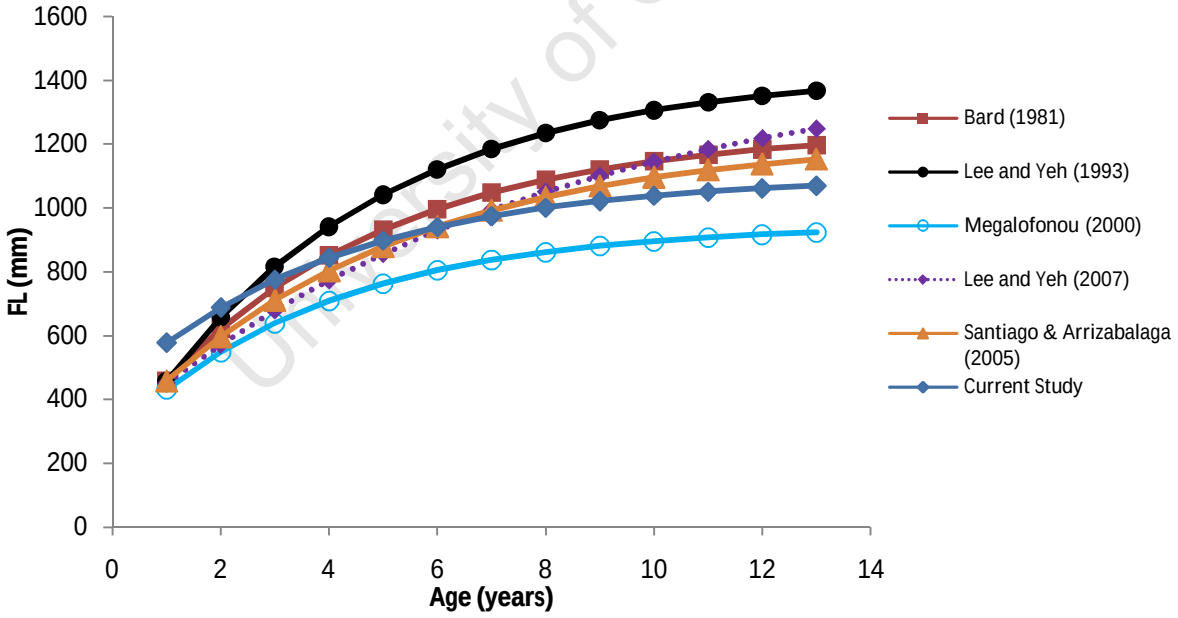

Figure 2.16: von Bertalanffy growth curves for albacore tuna (*Thunnus alalunga*) from the north Atlantic (Bard 1981), the south Atlantic (northwest region, Lee and Yeh 1993 and 2007), the Mediterranean Sea (Megalofonou 2000) and the south Atlantic (Cape Point region, current study).

The VBGF accounted for 50% of the variation within the data (R^2=0.49), a good fit considering the restricted length range of fish sampled. If sampling was carried out in definite seasons, ie. mid-summer and mid-winter, then the analysis of the marginal zone of otolithsshould show a significant relationship between hyaline or opaque ring deposition depending on season and accurate age validation could be tested. As it was, with sampling in May and October - at times of year when ring type deposition is likely changing, this relationship was not significant (Chi square=2.28, df=1, p=0.13).

The majority of fish sampled (70%) fall between 75 and 95 cm fork length. For this species it has been predicted that 50% will be mature at 90cm fork length or 5 years old (Bard 1981), so these are predominantly juvenile and sub-adult fish. The range of fish sampled was 58-114 cm but the lack of smaller fish affected the prediction of VBGF growth parameters and sampling in the future would better represent the popoulation by covering the lower and upper size classes. The commercial baitboat fishery predominantly catch fish ranging from 2 to 7 years old (ICCAT Report 2012) and may provide a source of smaller/younger fish for future studies. The longline vessels of Taiwan catch fish from age 0 to 10 years (ICCAT Report 2012), monitoring and sampling onboard foreign flagged longline vessels would provide samples of older, mature fish as well as pre-juveniles. It is therefore recommended to collect samples from these two fleets to consolidate the outcomes of the present study.

2.4.5 Stomach content analysis

The diet composition of juvenile and adult albacore tuna has been studied in various regions of the world oceans (Ortiz de Zárate 1987, Watanabe et al 2004, Pusineri et al 2005,Goñi et al 2011).

Pusineri et al (2005) looked at the stomach contents of juvenile albacore caught in commercial driftnet fishery in the Bay of Biscay, they found that fish were by far the most important prey items by number (86%) and mass (60%). Whereas fish occurred in 95.9% of stomachs of juvenile albacore in the Bay of Biscay they were only found in 36% of stomachs of albacore in this study. However it was *Maurolicus muelleri* that was the most numerous fish in both studies (79% - Bay of Biscay, 73% - current work).*M. muelleri* was found as accumulated material in the stomachs of albacore. Pusineri et al (2005) suggest that this small mesopelagic fish is likely to be digested within just a few hours and based on their hypothetical foraging rhythm for albacore that it would have been consumed during the evening or early night. In the case of albacore from South African waters this might also be true as fishers started catching fish as early as 6 am. It must be noted that all specimens of *M. muelleri* (56) occurred in only two stomachs from fish caught during October.

Crustaceans constituted 56% of the prey items by number and were found in 58% of the stomachs sampled in this study. The most numerous crustaceans were shrimp larvae, not further identifiable due to digestion, but these were found in only 5 stomachs with the majority of samples coming from a single fish and were thus not an important prey. The next most numerous crustacean was the hyperiid amphipod *Brachyscelus crusculum*, a pelagic crustacean, it was found 36% of albacore stomachs sampled. Potier et al (2007) found the same species in the diet of yellowfin tuna from the western equatorial Indian Ocean and it has been found in the stomachs of juvenile albacore between the subtropical and subarctic fronts of the north Pacific (Watanabe et al 2004).

Cephalopods were found in various states of digestion, from whole and fresh to fully digested beaks. The only species identified through upper and lower beak analysis was *Lycotheuthis lorigera* (Steenstrup 1875), a squid that is widely distributed from 30°N to 50°S (Clarke

1986). This is a mesopelagic species of squid that occurs on the shelfs off islands and continents (Nesis 1987). It was the most important prey species found in the stomachs of albacore in this study (PSIRI = 36.92%).

2.4.6 Stable isotope analysis

The carbon and nitrogen stable isotope composition of an organism is dependant on its diet, its trophic level and the isotopic signature at the base of the food web (DeNiro and Epstein 1981, Post 2002). SIA values are used as dietary tracers that provide the ability to predict trophic position and trophic habits of species (Peterson and Fry 1987, Layman et al 2007). $\delta^{13}C$ and $\delta^{15}N$ values fractionate in a predictable manner from dietery sources to consumers (Peterson and Fry 1987). The nitrogen isotopic ratio is predicted to increase between 2.5‰ to 5‰ per trophic level (Post 2002). The carbon isotopic ratio acts as an indicator of dietary sources of carbon as carbon isotopic values vary very little with trophic transfers (De Niro and Epstein 1981). Van der Lingen and Miller (2011) assumed mean trophic fractionation values of 0.4‰ per trophic level for $\delta^{13}C$ and 3.4‰ per trophic level for $\delta^{15}N$ in the southern Benguela.

The results obtained from the analysis of $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis offer an insight into the feeding habits and trophic position of albacore tuna in relation to yellowfin tuna. The $\delta^{15}N$ values are not significantly different between the two species indicating that they are feeding at a similar trophic level, even thoughthere was a large size difference between the fish sampled for the two species. This is indicative of the broad niche resource use by adult yellowfin tuna as seen in other areas of the world (Potier et al 2004, Potier et al 2007).

$\delta^{13}C$ Stable isotope values differed significantly between yellowfin and albacore tuna indicating that they are feeding on different dietary sources of carbon, and are possibly part of

two different food chains. Examination of the stomach contents of yellowfin is required to see if there is a difference in the prey targeted by each species. Yellowfin tuna exhibit two peaks in availability, one in May, one during October. Yellowfin could be entering South African waters from the Indian Ocean by travelling down the Agulhas current during a feeding migration. Alternatively they could be of tropical Atlantic origin.

It is plausible to consider that the two species are of different oceanic origin.The different nature of the environmental content of the Agulhas (a warm western boundary current) and Benguela (upwelling) systems could lead to the significant differences in $\delta^{13}C$ stable isotope values for albacore and yellowfin tuna.

The $\delta^{15}N$ stable isotope values for albacore and yellowfin tuna from this study were related to $\delta^{15}N$ values for other pelagic species within the southern Benguela current ecosystem calculated by van der Lingen and Miller (2011) (Figure 2.17).

Because there is a lack of $\delta^{15}N$ data for primary consumers in the southern Benguela region the sardine, *Sardinops sagax*, was used as the isotopic baseline to assign a trophic level (TL) to both species of tuna. Considering van der Lingen and Miller (2011), where the mean observed $\delta^{15}N$ value for sardine was 11.145‰ that corresponds to a TL of 2.99, and assuming an increase of 3.4‰ in $\delta^{15}N$ per trophic level (Post 2002), the TL for *T. alalunga* and *T. albacares* was calculated to be 3.80 and 3.76 respectively.

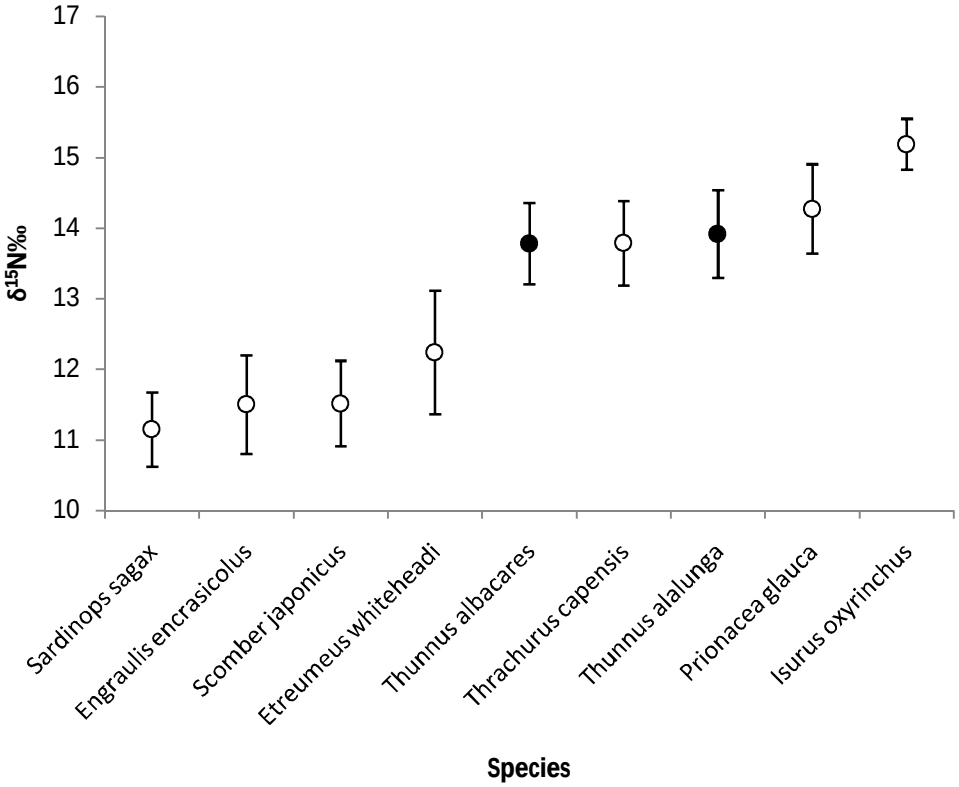

Figure 2.17: $\delta^{15}N$ stable isotope values for pelagic fish - sardine (*sardinops sagax*), anchovy (*Engraulis encrasiocolus*), chub mackerel (*Scomber japonicus*), round herring (*Etreumeus whiteheadi*), yellowfin tuna (*Thunnus albacares*), horse mackerel (*Trachurus capensis*) and albacore tuna (*Thunnus alalunga*) – and sharks –blue shark (*Prionacea glauca*), mako shark (*Isurus oxyrinchus*) – within the southern Benguela current ecosystem. (Filled circles indicate samples from the current study).

3. Conclusion

Sampling at angling competitions is a repeatable and cheap opportunity to acquire a moderate number of albacore and yellowfin tuna. A large portion of the observed size range of albacore tuna within South African waters can be covered, but fish smaller than 60 cm fork length are few in number as they are not prized specimens in competition. Angling competitions can provide wide spatial and seasonal coverage for sampling of both tuna species. Purchasing tuna from commercial fisherman is a far more costly alternative, and sampling on board of commercial vessels is unlikely as fish need to be properly handled so as not to reduce market value and measuring weight of the catch is inaccurate at sea. Working with organisations such as the South African National Tuna Association not only makes tuna available for research but also strengthens the connections between fishers and scientists and provides a platform to create awareness about changing fisheries and declining fish stocks.

Presenting the results of research such as that shown in this study is just the first step toward an on-going association that can lead to future work. Tagging operations could be facilitated by researchers at various universities around South Africa and implemented by regional fishing organisations or individual anglers in select areas of the coastline. A better understanding of the origin and spatial and temporal availability of albacore tuna within South African waters would benefit both the recreational and commercial fishery.

Albacore tuna are targeted in South African waters by commercial vessels from October through to May. The Agulhas retroflection zone acts as a shifting boundary between the Indian and Atlantic Ocean. In this area juvenile albacore from the Atlantic may get pushed into the Indian Ocean and fish from the Indian Ocean travelling down the Agulhas current may get pushed into the Atlantic. Once in the Atlantic albacore move up the South African

west coast and then offshore into the Atlantic in May. Juveniles arrive in October/November again.

Yellowfin tuna on the other hand exhibit two peaks in availability, one in May, one during October. These peaks coincide with the timing of national angling competitions targeting this species. Yellowfin could be entering South African waters from the Indian Ocean by travelling down the Agulhas current during a feeding migration. Alternatively they could be of tropical Atlantic origin.

The length-weight relationship for south Atlantic albacore from this study was central between the results south Atlantic and Indian Ocean albacore from other studies, as were the predicted von Bertalanffy growth parameters. Diet analysis of albacore tuna from South African waters did not show definite targeting of prey items endemic to either the Atlantic or Indian Ocean. A mixture of tuna from the Atlantic and Indo-Pacific oceans in South African waters has been shown for bigeye tuna (*Thunnus obesus*) (Chow et al 2000) and it is likely that this is the case for albacore tuna that are also a temperate species.The Indian Ocean Tuna Tagging Programme (IOTTP) tagged 35 997 bigeye tuna, the majority of which were released off the coast of Tanzania in the western Indian Ocean, results showed that a number of fish were recovered in the region south of Africa and a few as far north as Namibia (IOTC-SC15 2012).

There is a requirement to fill knowledge gaps arising from the lack of recent work on albacore tuna in South Africa. The information from historical studies can be used as a baseline for comparison with recent and future work derived from the restarting of local monitoring programs. A biological monitoring scheme that incorporates the domestic baitboat fishery, the recreational fishery and international longline fishery can provide data

that underpins the development of accurate stock assessment models. There is a potential for capacity building through the inclusion of volunteers at angling competitions.

Conventional tagging is cheap and a large number of fish can be tagged from the commercial baitboat fishery. More expensive electronic-archival tags could be used strategically in the longline fishery to provide detailed information on vertical and horizontal movement patterns with time.

A multidisciplinary approach coupling tagging movement data with genetic and stable isotope signatures and biological parameter analysis is required to make a connection between the Indian and Atlantic Ocean tuna populations and elucidate the stock structure of albacore and yellowfin tuna.

4. References

Aloncle, H. and Delaporte, F. (1973). Populations, croissance et migrations du germon (Thunnus alalunga) dans le nored-est Atlantique essai de synthèse. *Rev. Trav. Inst. Pêches marit.37*(1): 97-115.

Alonso, C., Arrizabalaga, H., and Restrepo, V. R. (2005).Contribution of a chapter on albacore tuna for the revised ICCAT field manual.*Col. Vol. Sci. Pap. ICCAT, 58*(5): 1646-1661

Altringham, J. D., and Shadwick, R. E. (2001). Swimming and muscle function. *Fish Physiology*, *19*(8): 313-344.

Ardill, J. D. (1995). Atlas of industrial tuna fisheries in the Indian Ocean.IPTP/95/AT/3, 144 p.

Arrizabalaga, H., Costas, E., Juste, J., González-Garcés, A., Nieto, B., and López-Rodas, V. (2004). Population structure of albacore *Thunnus alalunga* inferred from blood groups and tag-recapture analyses.*Marine Ecology Progress Series*, 282: 245-252.

Arrizabalaga, H., López-Rodas, V., Costas, E., and González-Garcés, A. (2007). Use of genetic data to assess the uncertainty in stock assessments due to the assumed stock structure: the case of albacore (*Thunnus alalunga*) from the Atlantic Ocean. *Fishery Bulletin, 105*(1): 140-146.

Bard, F. X. (1981). Le thon germon (*Thunnus alalunga*) de l'Océan Atlantique.Doctorate thesis in biology, Paris VI.329 pp.

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

Beamish, R. J., and Fournier, D. A. (1981).A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(8): 982-983.

Beardsley Jr. G. L. (1969).Proposed migrations of albacore, *Thunnus alalunga*, in the Atlantic Ocean. *Transactions of the American Fisheries Society*, *98*(4): 589-598.

Beckley, L. E., and Van Ballegooyen, R. C. (1992).Oceanographic conditions during three ichthyoplankton surveys of the Agulhas Current in 1990/91. *South African Journal of Marine Science*, *12*(1): 83-93.

Bosley, K. L., and Wainright, S. C. (1999). Effects of preservatives and acidification on the stable isotope ratios (15N: 14N, 13C: 12C) of two species of marine animals. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(11): 2181-2185.

Brown, S. C., Bizzarro, J. J., Cailliet, G. M., and Ebert, D. A. (2012).Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate,*Bathyraja aleutica* (Gilbert 1896). *Environmental Biology of Fishes*, *95*(1): 3-20.

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, *59*(2): 197-242.

Carroll, R. L.(1988). *Vertebrate Paleontology and Evolution.*New York: W. H. Freeman and Co.

Chang, W. Y. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences*, *39*(8): 1208-1210.

Chang, S. K., and Hsu, C. C. (1996). Adjusted Taiwanese longline CPUE of north Atlantic albacore stock from target species segregated catch data. *Col. Vol. Sci. Pap, ICCAT, 43*: 277-282.

Chen, I., Lee, P. F., and Tzeng, W. N. (2005).Distribution of albacore (*Thunnus alalunga*) in the Indian Ocean and its relation to environmental factors. *Fisheries Oceanography*, *14*(1): 71-80.

Chen, K. S., Shimose, T., Tanabe, T., Chen, C. Y., and Hsu, C. C. (2012).Age and growth of albacore (*Thunnus alalunga*) in the North Pacific Ocean. *Journal of Fish Biology*, *80*(6): 2328-2344.

Cheng, Z. L., Fengying, T., Hao, X., Liuxiong and Siquan, T. (2012). Age and Growth of Albacore Tuna (*Thunnus alalunga*) in the southern and central Indian Ocean based on Chinese observer data. Fourth Working Party on Temperate Tunas, Shanghai, China, 20-22 August 2012. IOTC-2012-WPTmT04-16 Rev_1.

Chow, S., Okamoto, H., Miyabe, N., Hiramatsu, K., and Barut, N. (2000). Genetic divergence between Atlantic and Indo-Pacific stocks of bigeye tuna (*Thunnus obesus*) and admixture around South Africa. *Molecular Ecology*, *9*(2): 221-227.

Clarke, M., R (ed) 1986. A Handbook for the Identification of Cephalopod Beaks. Clarendon Press, Oxford.

Collette, B. B., Reeb, C., and Block, B. A. (2001).Systematics of the Tunas and Mackerals (scombridae) in Block BA, Stevens ED. 2001.*Tuna: physiology, ecology, and evolution.* San Diego, California, London: Academic Press.

Collette, B. B., and Nauen, C. E. (1983).*FAO Species Catalogue.Scombrids of the World.* Rome: FAO.

Crosnier, A and Forest, J.(1973). Les crevettes profondes de L'Atlantique oriental tropical.*Faune Tropicale.*,(*19*): 1 – 409.

De Jager, B., Nepgen, C. S., and Van Wyk, R. J. (1963). A preliminary report on tuna in west coast waters of South Africa. *S. Afr. Shipp. News Fish.Ind. Rev.* 18: 4, 5 & 6.

De Niro, M. J., and Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, *45*(3): 341-351.

Department of Agriculture, Forestry and Fisheries (DAFF).(2012). *Status of the South African Marine Fishery Resources* 2012.

Dickson, K. A., and Graham, J. B. (2004).Evolution and consequences of endothermy in fishes. *Physiological and Biochemical Zoology, 77*(6): 998-1018.

Dotson, R. C. (1976). Minimum swimming speed of albacore, *Thunnus alalunga*. *Fishery Bull*, *74*: 955-960.

Ely, B., Viñas, J., Bremer, J. R. A., Black, D., Lucas, L., Covello, K., and Thelen, E. (2005). Consequences of the historical demography on the global population structure of two highly migratory cosmopolitan marine fishes: the yellowfin tuna (*Thunnus albacares*) and the skipjack tuna (*Katsuwonus pelamis*). *BMC Evolutionary Biology*, *5*(1): 19.

Farley, J., and Clear, N. (2008).Preliminary study of age, growth, and spawning activity of albacore in Australia's Eastern Tuna & Billfish Fishery. *WCPFC SC4 BI-IP-1, Port Moresby, Papua New Guinea.*

Fonteneau, A. (2004). An overview of Indian Ocean albacore: fisheries, stocks and research. IOTC-2004-WPTMT-02.

Fonteneau, A. (2008). An overview of albacore tuna in the Indian Ocean: biology, fisheries and stock status. IOTC-2008-WPTe-07.

Froese, R., and Pauly, D. (eds). (2006). Fishbase. *World Wide Web electronic publication. Available at: www. fishbase. org, version (06/2006)*.

Fromentin, J. M., and Fonteneau, A. (2001). Fishing effects and life history traits: a case study comparing tropical versus temperate tunas. *Fisheries Research, 53*(2): 133-150.

Gibbs, R. H., and Collette B. B. (1967).Comparative anatomy and systematics of the tunas, genus *Thunnus*.*Fish. Bull. 66*(1): 65-130.

Goñi, N., Logan, J., Arrizabalaga, H., Jarry., M and Lutcavage, M. (2011). Variability of albacore (*Thunnus alalunga*) diet in the Northeast Atlantic and Mediterranean Sea.*Mar. Biol.* 158: 1057-1073.

Graham, J. B., and Dickson, K. A. (1981).Physiological thermoregulation in the albacore *Thunnus alalunga*. *Physiological Zoology*, 470-486.

Gunn, J. S., Clear, N. P., Carter, T. I., Rees, A. J., Stanley, C. A., Farley, J. H., and Kalish, J. M. (2008). Age and growth in southern bluefin tuna, *Thunnus maccoyii* (Castelnau): Direct estimation from otoliths, scales and vertebrae. *Fisheries Research, 92*(2): 207-220.

Gunther, A. (1860). Catalogue of the *acanthopterygian* fishes in the collection of the British Museum 2. London: British Museum.

Havard Duclos, F. (1973). La pêche au germon (Thunnus alalunga) dans le Golfe de Gascogne. Influence de la temperature sur le déplacement des mattes. *Col. Vol. Sci. Pap., ICCAT.Vol* I: 341-370.

Haung, C. S., Wu, C. L., and Su, W. C. (1990) Age and Growth of Indian Ocean albacore, *Thunnus alalunga*, by scales. FAO IPTP/TWS/90/53 111-122.

Horne, C. (1959). Big Game Fishing in South Africa.Cape Town: Timmins.

Hsu, C. C. (1999). The length–weight relationship of Albacore, *Thunnus alalunga*, from the Indian Ocean. *Fisheries Research, 41*(1): 87-92.

ICCAT Albacore Species Group.(1996). Report of the final meeting of the ICCAT albacore research program (Sukarrieta, Vizcaya, Spain, 1-8 June, 1994).*Col. Vol. Sci. Pap., ICCAT, 43*:1-140.

ICCAT Report.(2008). Report of the standing committee on research and statistics (SCRS) (Madrid, Spain, September 29 to October 3, 2008).

ICCAT Report.(2011). Report of the standing committee on research and statistics (SCRS) (Madrid, Spain, October 3 – 7, 2011).

ICCAT Circular # 5058 (2011). Recommendations and resolutions adopted at the 2011 commission meeting, Madrid, Spain.

ICCAT Report.(2012). Report of the 2011 ICCAT South Atlantic and Mediterranean Albacore Stock Assessment Sessions.*Col. Vol. Sci. Pap. ICCAT, 68*(2): 387-491.

ICCAT Statistical Bulletin. (2013). Statistical Bulletin, Volume 41 (2), 1950 – 2011.

IOTC–SC15 2012.Report of the Fifteenth Session of the IOTC Scientific Committee. Mahé, Seychelles, 10–15 December 2012. IOTC–2012–SC15–R[E]: 288 pp.

Jobling, M. (1987). Influences of food particle size and dietary energy content on patterns of gastric evacuation in fish: test of a physiological model of gastric emptying. *Journal of Fish Biology*, *30*(3): 299-314.

Jobling, M. (1994).Fish Bioenergetics. Chapman and Hall, London.

Kerwath, S. E., Winker, H., and West, W. M. (2012).Standardization of the catch per unit effort for albacore (*Thunnus* alalunga) for the South African tuna-pole (baitboat) fleet for the time series 1999-2010.*Col. Vol. Sci. Pap., ICCAT, 68*(2), 604-614.

Koto, T. (1969). Distribution and movement of the albacore in the Indian and the Atlantic Oceans based on the catch statistics of Japanese tuna longline fishery. *Bull. Far Seas Fish. Res. Lab, 1*: 115-129.

Kroese, M. (1999).South African Tuna Fisheries.IOTC-1999-WPDCS99-12.

Laurs, R. M., Fiedler, P. C., and Montgomery, D. R. (1984). Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep Sea Research Part A. Oceanographic Research Papers, 31*(9), 1085-1099.

Laurs, R. M., Nishimoto, R., and Wetherall, J. A. (1985).Frequency of increment formation on sagittae of north Pacific albacore (*Thunnus alalunga*). *Canadian Journal of Fisheries and Aquatic Sciences*, *42*(9): 1552-1555.

Layman, C. A., Arrington, D. A., Montaña, C. G., and Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, *88*(1): 42-48.

Le Gall, J. Y. (1974). Exposé synoptique des données biologiques sur le Germon *Thunnus alalunga* (Bonnaterre, 1788) de l'Océan Atlantique. FAO Synopsis sur les Pêches, 109: 1-70

Lee, Y. C., and Liu, H. C. (1992).Age determination, by vertebra reading, in Indian Ocean albacore, *Thunnus alalunga*Bonnaterre.*J. Fish. Soc. Taiwan, 19*(2): 89-102.

Lee, L. K., and Yeh, S. Y. (1993). Studies on the age and growth of South Atlantic albacore (*Thunnus alalunga*) specimens collected from Taiwanese longliners. *Col. Vol. Sci. Pap., ICCAT, 40*(2): 354-360.

Lee, L.K., and Yeh, S. Y. (2007). Age and growth of south Atlantic albacore – a revision after the revelation of otolith daily ring counts. *Col. Vol. Sci. Pap.,ICCAT,* (2): 443-456.

Lehodey, P., and Leroy, B. (1999). Age and growth of yellowfin tuna (*Thunnus albacares*) from the western and central Pacific Ocean as indicated by daily growth increments and tagging data. *WP YFT-2, SCTB, 12*: 16-23.

Lewis, A. D. (1990). South Pacific albacore stock structure: a review of available information. In *WP/5 3rd South Pacific Albacore Workshop*.

Maunder, M. N., Sibert, J. R., Fonteneau, A., Hampton, J., Kleiber, P., and Harley, S. J. (2006). Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES Journal of Marine Science: Journal du Conseil*, *63*(8): 1373-1385.

Megalofonou, P. (1991). Size distribution, length-weight relationships, age and sex of albacore, *Thunnus alalunga*Bonn., in the Aegean Sea. *Col. Vol. Sci. Pap.,ICCAT,* (33): 154-162.

Megalofonou, P. (2000). Age and growth of Mediterranean albacore. *Journal of Fish Biology*, *57*(3): 700-715.

Ménard, F., and Marchal, E. (2003). Foraging behaviour of tuna feeding on small schooling *Vinciguerria nimbaria* in the surface layer of the equatorial Atlantic Ocean. *Aquatic Living Resources, 16*(03): 231-238.

Ménard, F., Labrune, C., Shin, Y. J., Asine, A. S., and Bard, F. X. (2006). Opportunistic predation in tuna: a size-based approach. *Marine EcologyProgress Series, 323*: 223-231.

Mendoza, R. P. R. (2006). Otoliths and their applications in fishery science.*Ribarstvo, 64*(3): 89-102.

Monod, T. (1968).*Le Complexe Urophore des Poissons Téléostéens.*Mémoires de L'Institut Fondamental D'Afrique Noire.Ifan-Dakar.

Morita, S. (1978).On the relationship between albacore stocks of the South Atlantic and Indian Ocean. *Col. Vol. Sci. Pap.,ICCAT, 7*(2): 232-237.

Motulsky, H and Christopoulos, A. (2004). Fitting models to biological data using linear and nonlinear regression: a practical guide to curve fitting. Oxford University Press, Inc. 198 Madison Avenue, New York, New York 10016.

Nakamura, H. (1969). Tuna Distribution and Migration. London: The Whitefriairs Press Ltd, 76 pp.

Nepgen, C. S. De V. (1971). Review of South African tuna fisheries and research. *ICCAT Report for Biennial Period, 1970-71.* Part 2: 114-116.

Nesis, K. N. (1987). Cephalopods of the world: squid, cuttlefish, octopuses and their allies. *TFH Publication, Neptune City, New Jersey*.

Newcombe, H. C. (2011). Contribution towards the development of a management plan for the baitboat and sport fishery for tuna in South Africa.Masters dissertation, Rhodes University, 159 pp.

Ortiz de Zárate, V. (1987). Datos sobre la alimentación del Atún blanco (Thunnus alalunga) juvenil capturado en el Golfo de Vizcaya. *Col. Vol. Sci. Pap. ICCAT, 26*(2), 243-247.

Ortiz De Zárate, V., and Cort J. L. (1998). Albacore (*Thunnus alalunga*, Bonnaterre) stock structure in the Atlantic Ocean, as inferred from distribution and migration patterns. Proceedings of the ICCAT Tuna Symposium (Beckett, J.E. ed.), volume 1: 251-260.

Otsu, T., and Hansen, R. (1962). Sexual maturity and spawning of the albacore in the central south Pacific Ocean. *Fish. Bull.* 67: 151-162.

Otsu, T., and Sumida, R. F. (1968). Distribution, apparent abundance, and size composition of albacore (*Thunnus alalunga*) taken in the longline fishery

based in American Samoa, 1954-65. *US Nat. Mar. Fish.Serv., Fish. Bull*, *67*(1): 47-69.

Pauly, D. (1978).A preliminary compilation of fish length growth parameters.*Ber.Inst. Meereskd.*Christian-Albrechts-Univ. Kiel. 55: 1-200.

Penney A. J., Krohn R.G., and Wilke C. G. (1992).A description of the South African tuna fishery in the southern Atlantic Ocean.*Col. Vol. Sci.Pap., ICCAT,* 39: 247–257.

Penney, A. J. (1994). Morphometric relationships, annual catch-at-size for South African-caught South Atlantic albacore (*Thunnus alalunga*).*Col. Vol. Sci. Pap., ICCAT,* XLII (1): 371-382.

Penney A. J., Yeh S. Y., Kuo C. L., and Leslie R. W. (1998).Relationships between albacore (*Thunnus alalunga*) stocks in the southern Atlantic and Indian Oceans.*Col. Vol. Sci.Pap., ICCAT,* 50: 261–271.

Penney A. J., and Griffiths M. H. (1999).A first description of the developing South African pelagic longline fishery.*Col. Vol. Sci.Pap., ICCAT,* 49: 162–173.

Penrith, M. J. G. (1963). The systematics and biology of the South African Tunas. Masters Dissertation, University of Cape Town.

Peterson, B. J., and Fry, B. (1987).Stable isotopes in ecosystem studies.*Annual Review of Ecology and Systematics, 18:* 293-320.

Post, D. M. (2002).Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, *83*(3), 703-718.

Postel, E. (1964). Surdeux lots de germon (*Germe alalunga*) captures dans le Golfe de Guinée par les palangriers japonais. Cahiers ORSTOM Ser. *Océanographic2*(2): 55-60.

Potier, M., Marsac, F., Lucas, V., Sabatié, R., Hallier, J-P and Ménard, F. (2004).Feeding Partitioning among Tuna Taken in Surface and Mid-water layers: The Case of Yellowfin (*Thunnus albacares*) and Bigeye (*T. obesus*) in the Western Tropical Indian Ocean.*Western Indian Ocean J. Mar. Sci, 3*(1): 51-62.

Potier, M., Marsac, F., Cherel, Y., Lucas, V., Sabatié, R., Maury, O., and Ménard, F. (2007). Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. *Fisheries Research, 83*(1): 60-72.

Pusineri, C., Meynier, L., Spitz, J., and Ridoux, V. (2003). Differential digestion rates of dolphin prey: observational and experimental bases for an improved dietary analysis procedure. In *17th Conference of the European Cetacean Society Abstract Book*, pp. 194-195. Ed. By ECS, La Palmas de Gran Canaria, 285 pp.

Pusineri, C., Vasseur, Y., Hassani, S., Meynier, L., Spitz, J., and Ridoux, V. (2005). Food and feeding ecology of juvenile albacore, Thunnus alalunga, off the Bay of Biscay: a case study. *ICES Journal of Marine Science: Journal du Conseil, 62*(1): 116-122.

Reiner, F. (1996). Catálogo dos peixes do Arquipélago de Cabo Verde. Publicações avulsas do IPIMAR No. 2, 339 pp.

Santiago, J. (1993). A new length-weight relationship for the North Atlantic albacore. *Col. Vol. Sci. Pap., ICCAT, 40*(2): 316-319.

Santiago, J. (2004). Dinámica de la población de atún blanco (*Thunnus alalunga* Bonaterre 1788) del Atlántico Norte. Tesis Doctoral, Univ. París Vasco 354 pp.

Santiago, J., and Arrizabalaga, H. (2005).An integrated growth study for North Atlantic albacore (*Thunnus alalunga* Bonn. 1788). *ICES Journal of Marine Science: Journal du Conseil*, *62*(4): 740-749.

Sauer W. H. H., Penney A. J., Erasmus C., Mann B. Q., Brouwer S. L., Lamberth S. J., and Stewart T. J. (1997). An evaluation of attitudes and responses to monitoring and management measures for the South African boat-based linefishery. *South African Journal of Marine Science* 18: 147–163.

Sauer, W. H. H., Hecht, T., Britz, P. J., and Mather D. (2003). An Economic and Sectoral Study of the South African Fishing Industry 2: Fishery Profiles. *Report prepared for Marine and Coastal Management by Rhodes University*, Grahamstown.

Sea fisheries report no. 47.(1979). South African Division of Sea Fisheries, Investigational Report No. 47.

Schaefer, K. M. (1998). *Reproductive biology of yellowfin tuna (Thunnus albacares) in the eastern Pacific Ocean*. Inter-American Tropical Tuna Commission, 20: 135 – 163.

Schaefer, K. M. (2001). Reproductive Biology of Tunas.In: Block B. A., Stevens E. D., 2001. *Tuna: physiology, ecology, and evolution*. San Diego, California, London: Academic Press, pp. 225 – 270.

Shannon, L. V. (1987). The tunas of the Benguela region off southern Africa - A synthesis.*Col. Vol. Sci. Pap., ICCAT, 26*(2): 566-581.

Shin, Y. J., and Cury, P. (2001).Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model.*Aquatic Living Resources*, *14*(2): 65-80.

Shin, Y. J., and Cury, P. (2004).Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing.*Canadian Journal of Fisheries and Aquatic Sciences, 61*(3): 414-431.

Shiohama, T. (1971).Studies on measuring changes in the character of the fishing effort of the tuna longline fishery.Concentrations of the fishing effort to particular areas and species in the Japanese Atlantic fishery. *Bull. Far Seas Fish. Res. Lab, 5*: 107-130.

Smale, M. J., Watson, G. and Hecht, T. (1995).Otolith atlas of southern African Marine fishes. Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology 1: 1–232.

Smith, M.M., and Heemstra, P. C. (eds) (1991). Smiths' Sea Fishes.1st edition.Southern Book Publishers, Johannesburg, 1048 pp.

Sund, P. N,, Blackburn, M., and Williams, F. (1981). Tunas and their Environment in the Pacific Ocean: A Review.*Oceanogr. Mar. Biol. Ann. Rev.,* 19: 443-512.

Takagi, M., Okamura, T., Chow, S., and Taniguchi, N. (2001). Preliminary study of albacore (*Thunnus alalunga*) stock differentiation inferred from microsatellite DNA analysis. *Fishery Bulletin-National Oceanic and Atmospheric Administration*, *99*(4): 697-701.

Talbot, F. H., and Penrith, M. J. (1968).The tunas of the genus *Thunnus* in South African waters.Part 1.Introduction, systematics, distribution and migrations.*Ann. S. Afr. Mus, 52*(1): 1-41.

Ueyanagi, S. (1969).Observations on the distribution of tuna larvae in the Indo-Pacific Ocean with emphasis on the delineation of the spawning areas of albacore, *Thunnus alalunga*. *Bull. Far Seas Fish. Res. Lab., 2:* 177-256.

Ueyanagi, S. (1971).Larval distribution of tunas and billfishes in the Atlantic Ocean.*FAO Fish. Report* 71 (2): 297-305.

Uozumi, Y. (1996). An historical review of Japanese longline fishery and albacore catch in the Atlantic Ocean. *Col. Vol. Sci.Pap., ICCAT, 43*: 163-170.

van der Elst, R. (1981). A guide to the common sea fishes of southern Africa. C. Struik, Cape Town, 376 pp.

van der Elst, R., and Bullen, E. (1987). Tagging News, No. 3, Summer 86/87.Published by Oceanographic Research Institute of the South African Association for Marine Biological Research, P. O. Box 736, Durban 4000.

van der Lingen, C. D., and Miller, T. W. (2011). Trophic dynamics of pelagic nekton in the southern Benguela current ecosystem: Calibrating trophic models with stable isotope analysis. *Interdiciplinary Studies on Environmental Chemistry-Marine Environmental Modelling & Analysis*, pp. 85-94.

Watanabe, H., Kubodera, T., Masuda, S., and Kawahara, S.(2004).Feeding habits of albacore, *Thunnus alalunga*, in the transition region of the central North Pacific. *Fisheries science, 70*(4): 573-579.

West, W. M., Kerwath, S. E., da Silva, C., Wilke, C. G., and Marsac, F. (2012). Horizontal and vertical movements of swordfish tagged with pop up-satellite transmitters in the south-west Indian Ocean, off South Africa. IOTC-2012-WPB10-16.

Yeh, S. Y., Hui, C. F., Treng, T. D., and Kuo, C. L. (1996). Indian Ocean albacore stock structure studies by morphometric and DNA sequence methods. IOTC Proceedings, 6th Expert Consultation on Indian Ocean Tunas. pp. 258-263.

Yeh, S. Y., Treng, Y. D., Hui, C. F., and Penney A. J. (1997). Mitochondrial DNA sequence analysis on albacore, *Thunnus alalunga*, meat samples collected

from the waters off western South Africa and the eastern Indian Ocean. *Col. Vol. Sci. Pap., ICCAT, 46*(3): 152-159.

Zar, J. H. (2009). Biostatistical Analysis, 5th Edition. Pearson International Edition.