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Estimating Movement Rates of Atlantic Ocean Tropical Tunas, *Katsuwonus Pelamis*, *Thunnus Albacares*, and *T. Obesus*, from Tagging Data

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ESTIMATING MOVEMENT RATES OF ATLANTIC OCEAN TROPICAL TUNAS,
KATSUWONUS PELAMIS, *THUNNUS ALBACARES*, AND *T. OBESUS*, FROM
TAGGING DATA

By

Michelle L. Sculley

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

December 2016

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TROPICAL TUNAS, *KATSUWONUS PELAMIS*, *THUNNUS*
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Estimating Movement Rates from Atlantic
Ocean Tropical Tunas, *Katsuwonus pelamis*,
Thunnus albacares, and *T. obesus* from
Tagging Data

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Tagging programs are valuable sources of information about the population dynamics and fisheries interactions for a stock or population. Information gained from these programs can be incorporated into stock assessments to reduce uncertainty in the current stock status. Large scale tagging programs can provide important insights on the stock structure and the movements of individuals. While tagging on the tropical tunas skipjack, *Katsuwonus pelamis*, yellowfin, *Thunnus albacares*, and bigeye tuna, *T. obesus*, has occurred in the Atlantic Ocean since the 1950s, these tagging studies have been small and localized in nature. A spatially explicit Bayesian was used to analyze historical Atlantic conventional tag data and showed that the tagging data available provide information on regional movements within the Eastern Atlantic Ocean, but due to fewer tag releases and returns in the Western Atlantic, basin-wide parameters are not estimable. Catch and effort data suggest that these movements are seasonal. A large scale tagging program is currently being implemented in the Atlantic Ocean by the International Commission for the Conservation of Atlantic Tunas (ICCAT). A simulation framework was developed to model ICCAT's Atlantic Ocean Tuna Tagging Program (AOTTP) and provide recommendations for the statistical design of the program. This simulation framework was used to simulate the release of two types of electronic tags, data storage tags (DST) and popup satellite archival tags (PSATs) on yellowfin and bigeye tuna. A

Bayesian space-state model was used to estimate movement rates, fishing mortality, and natural mortality from the simulated electronic data and simulated conventional tags. Fishing and natural mortality parameter estimates were very similar from both types of electronic tags. For stock assessment models that incorporate age-specific mortality, tagging programs can be used to provide parameter estimates. Using conventional tag data simulated using an age-specific fishing and natural mortality in a spatially-explicit simulation framework, a Bayesian space-state model was used to estimate mortality as age-specific parameters and age-constant parameters. Model results indicated that when the underlying population dynamics have significant age structure, assuming natural and fishing mortality parameters were constant across age classes resulted in significantly biased parameter estimates. Parameters were better estimated when allowed to vary with age. Fishing mortality was estimated as region and age independent parameters which had significant variability, although it is expected that assuming a functional relationship between fishing mortalities at age would improve the accuracy and precision of the parameter estimates. The simulations provided several recommendations to help the AOTTP meet the goals of the program.

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CHAPTER 1: AN OVERVIEW OF THE ATLANTIC TROPICAL TUNA FISHERIES AND TAGGING PROGRAMS

Fishing on tropical tunas

Over 4.5 million tons of tuna are caught each year in the global fisheries, of which tropical tunas constitutes 3 million tons (FAO, 2012). These tropical tunas, consisting of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*T. obesus*), are caught throughout all of the world's oceans, between 50°N and 50°S (Pallares *et al.*, 1998). Approximately 60% of the tropical tuna catch is skipjack tuna, which are typically caught in surface gears such as purse seines and baitboats. However, skipjack is generally sold to canneries which offer a low price per kilogram of fish (<1USD). Bigeye tuna, while only contributing to 10% of the tropical tuna catch, accounts for 40% of the total value of tuna sold worldwide. Bigeye tuna are typically caught on longline gear and many are sold to Japanese markets for sashimi and are worth >10USD per kilogram. Juvenile bigeye tuna, however, are caught in surface gears like skipjack and yellowfin tuna, and sold to canneries (Fonteneau *et al.*, 2004). Yellowfin tuna are caught in both the surface fisheries and longline fisheries and are generally sold to canneries when small and sold as tuna steaks when large (Anonymous, 2011). The Pacific Ocean contributes the majority of the tuna catch, with approximately 78% of the total, while the Atlantic contributes only 10% of the total tuna catch.

The tropical tuna fisheries have existed commercially since the 1950s in the global oceans, although recent changes in the fishing methods have caused a significant change in the species composition of the surface fisheries' catch. While the Atlantic Ocean only produces 10% of the world's tropical tuna catch, the surface fisheries are an important component of many coastal countries' economies (Million, 2013). In Cote

d'Ivoire, fish accounts for 50% of the animal protein consumed by the population and landings from the tropical tuna fishery contribute to the majority of the catch in the country (Amandè *et al.*, 2016).

The surface fisheries in the Atlantic Ocean were established in the early 1950s by French fisherman in Dakar followed by the development of the Ghanaian fleet in the 1970s (Wise, 1987). The catch at this time was primarily yellowfin tuna. The majority of the tropical tuna catch in the Atlantic comes from the Eastern Atlantic, with the Gulf of Guinea the dominant fishing grounds (Anonymous, 2011). In addition to these tropical fisheries, several seasonal baitboat fisheries were developed in Senegal, Madeira, the Azores Islands, and the Canary Islands. These seasonal catches are likely due to seasonal migrations of the tuna throughout the Eastern Atlantic (Fonteneau *et al.*, 2004).

Tropical tunas, along with a variety of other fish species, naturally aggregate under floating objects like logs, seaweed, etc. which provide prey and protection from predators (Marsac *et al.*, 2000). In the 1980s, fishermen in the Eastern Atlantic began deploying artificial fish aggregating devices (FADs) which were typically made of cheap materials but served to aggregate tunas to make them easier to catch (Dagorn *et al.*, 2013). These FADs can be anchored or drifting and are typically constructed on bamboo strips interwoven with netting. They are around 5-7 meters in length, 1-2 meters in width, and are fitted with radio devices so vessels can return to them (Bannerman and Bard, 2002). Anchored FADs are used extensively around islands like those in the Caribbean (Reynal *et al.*, 2008), while drifting FADs are primarily deployed in the Eastern Atlantic (Dempster and Taquet, 2004). The use of FADs in the surface tuna fisheries exploded in the 1990s, and currently there are thousands of FADs used in the

worlds' oceans. The release of artificial FADs has increased the density of floating objects 2-40 times the density of natural floating objects (Dagorn *et al.*, 2013). In 2013 the Spanish purse seine fleet alone deployed close to 6,000 new FADs in the tropical Atlantic (Delgado de Molina *et al.*, 2014).

FADs allow for a higher catch per unit effort for fisherman. Approximately 90% of all sets on FADs are successful; whereas only 50% of sets on free schools are successful (Fonteneau *et al.*, 2000a). The surface fisheries prior to the use of FADs caught primarily free schools of yellowfin and skipjack tuna, however, the amount of juvenile bigeye tuna caught in these fisheries has increased drastically since the 1990s with 90% of FAD sets containing bigeye tuna (Fonteneau *et al.*, 2004). These changes, which have been observed in all oceans, may be worsening the impact of fishing on the stocks of the tropical tunas and on the ecosystem, as FADs attract other organisms that may also be impacted by fishing on FADs (Delgado de Molina *et al.*, 2014).

Another method of catching tropical tunas in the Atlantic is the use of baitboats at drifting FADs by fisherman out of Dakar (Fonteneau and Diouf, 1994; Hallier and Delgado de Molina, 2000). This method allows the baitboat to maintain a school of fish underneath it and continuously fish from the school, often for months at a time. This has allowed baitboats in this area to greatly increase their catch per unit effort (Fonteneau and Diouf, 1994; Hallier and Delgado de Molina, 2000; Fonteneau *et al.*, 2004).

Yellowfin Tuna

Yellowfin tuna in the Atlantic are distributed in the subtropical and tropical surface waters between 45°N and 45°S. Juvenile yellowfin tuna tend to remain in the equatorial region and in the coastal areas. Adults and pre-adults are often found in the

pelagic waters. The largest fishery for yellowfin tuna are the purse seine fleets in the eastern Atlantic and Gulf of Guinea (**Figure 1.1**). The total catch in 2010, the most recent stock assessment, was 100 000 tons (t), which is a 48% reduction in catch from the peak of 190 000t in 1990 (Anonymous, 2011).

Catches by purse seiners account for 68% of the total Atlantic catch (Anonymous, 2010a). In general, large adult yellowfin tuna are caught in the first quarter and in free (non-associated) schools. Small yellowfin tuna are caught throughout the rest of the year associated with FADs; these catches are often in cooperation with baitboat operations. The amount of catch on FADs versus free schools varies with each fleet. Ghanaian purse seine catches are 80-85% on FADs while the European Union fleets tend to only fish on FADs 40-45% of the time. In the western Atlantic, the Brazilian and Venezuelan purse seine fleets catch small amounts of adult yellowfin (Anonymous, 2010a).

Baitboats catch primarily juvenile yellowfin tuna in mixed species schools with similar sized skipjack tuna and juvenile bigeye tuna. The largest baitboat catches are from the Ghanaian baitboat fleet and 70-80% of all baitboat catches are on FADs (Anonymous, 2010a). In the western Atlantic, Brazil and Venezuela baitboats catch small yellowfin tuna associated with skipjack tuna. The longline fleets catch large (>100cm) adult yellowfin tuna throughout their distribution in the Atlantic Ocean. They account for the smallest proportion of Atlantic catch (Anonymous, 2010a).

Skipjack Tuna

Skipjack tuna are found throughout the tropical and subtropical waters of the Atlantic Ocean. They are caught almost exclusively in the surface gears, baitboats and purse seines (**Figure 1.2**, Anonymous, 2014b). Skipjack account for the highest catches

of tropical tuna in the Atlantic, with over 267 000t in 2012, a 42% increase in catch compared to the previous five years (Anonymous, 2014b). Approximately 90% of the skipjack catch is on FADs and 85% of the catch is from the eastern Atlantic Ocean. In the western Atlantic, skipjack are caught by the Brazilian baitboat fishery and the Venezuelan purse seine fishery, however these catches are typically <30,000t (Meneses de Lima *et al.*, 2000, Anonymous, 2014b).

Bigeye tuna

Bigeye tuna have the smallest reported catches in the Atlantic of the tropical tunas. Catches in 2014 were 66 000t, less than half of those reported at their peak, 135 000t in 1993. There have been significant increases in juvenile bigeye tuna which have been caught in the surface fisheries since FAD fishing became more predominant in the 1980s and 1990s. In 2014, almost half of the catch was juvenile fish with baitboat fleets catching 2800t, purse seiners catching 23 000t and longline fleets catching 33 000t of bigeye tuna (**Figure 1.3**).

Longline catches are almost exclusively large adult bigeye tuna over 100cm. The Japan and Chinese Taipei fleets account for 46% of the longline catch (Anonymous, 2016b). The surface fisheries, baitboats and purse seiners, catch juvenile bigeye tuna (<100cm) in mixed species schools with skipjack and yellowfin tuna around FADs. While they are not a primary target, their catches can be significant and impact the future sustainability of the stock. Bigeye tuna are also caught seasonally in temperate fisheries such as the Azores and Canary Islands by baitboats. Bigeye tuna are not caught in large numbers in the surface fisheries in the western Atlantic (Anonymous, 2016b).

Stock Assessments

Atlantic tuna and tuna-like species are currently managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT), a regional fisheries management organization (RFMO) established in 1966. It is made up of 50 contracting parties (countries) and four cooperating parties who contribute to the management of these species by contributing fisheries catch and effort data and scientific expertise for stock assessments. The tropical tuna stocks are assessed approximately every five years to determine their status: if they are overfished and if overfishing is occurring. According to their most recent stock assessments, the yellowfin stock is overfished (Anonymous, 2011), the skipjack stocks are not overfished and overfishing is not occurring (Anonymous, 2014b), and the bigeye stock is overfished and overfishing is occurring (Anonymous, 2016b). However, these assessments contain high levels of uncertainty due to the limited information on key population parameters such as natural mortality, catchability, and migration/movement (Million, 2013). The implementation of tagging programs in the Pacific and Indian Oceans has helped reduce the uncertainty associated with these parameters and the tagging data have been used in more recent stock assessments in these regions. A similar incorporation of tagging data into the Atlantic Ocean stock assessments would likely decrease the uncertainty in the stock status of each of the tropical tunas.

Tagging of Tropical Tunas

Tagging programs have been undertaken by fishing nations since the 1950s in order to better understand the dynamics of tropical tunas. In the Western Pacific Ocean

alone over 800 000 tuna have been tagged and released. The South Pacific Commission Skipjack Survey and Assessment program aimed at assessing tuna movement around seamounts in the western Pacific (Sibert and Hampton, 2003). A large scale Western Pacific Region Tuna Tagging Program tagged over 8 000 bigeye tuna, 98 000 skipjack tuna, and 40 000 yellowfin tuna (Sibert and Hampton, 2003). Additionally, tagging projects in the Eastern Pacific using acoustic tags and conventional tags have been used around the Hawaiian Islands to observe the movement of yellowfin and bigeye tuna around anchored FADs (Itano and Holland, 2000).

More recently, a large scale tuna tagging program in the Indian Ocean (Regional Tuna Tagging Project – Indian Ocean or RTTP-IO) took place from 2002 – 2009 tagging over 200 000 tropical tunas. This program consisted of tagging on baitboats primarily in the Western Indian Ocean. To date, 16% of the tagged tunas have been recovered, the majority of which have been from purse seine vessels (Eveson *et al.*, 2012). In all tagging programs, a very small number of tag returns have been reported from longline fisheries (Leroy *et al.*, 2015). The RTTP-IO tagged 63 000 yellowfin tuna, 35 000 bigeye tuna, and 100 000 skipjack tuna with the goal to improve the ability of the interested states to manage the tuna fisheries in the Indian Ocean. This program was able to produce new insights into the growth and movement of tropical tunas in the Indian Ocean (Dortel *et al.*, 2012).

Atlantic Ocean Tagging Programs

Several small tagging programs for tuna have taken place in the Atlantic Ocean. These include the International Skipjack Year Program (ISYP), Yellowfin Tuna Year Program (YFTYP), Bigeye Tuna Year Program (BETYP), and the Mattes de thons

Associées aux Canneurs (MAC) program in the eastern Atlantic. In the western Atlantic tagging began in the 1950s when the US and South Africa began tagging tuna and has occurred almost every year since, involving different countries (Million, 2013). The Cooperative Tagging Program from the Southeast Fisheries Science Center began tagging tuna and billfish in 1954 and has since tagged over 200 000 fish. Overall, there have been 72 000 tropical tunas tagged in the Atlantic Ocean and 11 000 recoveries (Million, 2013).

The International Skipjack Year Program (ISYP) was executed in 1978-1982 by ICCAT with the goal of determining if catches of skipjack could be increased in the Atlantic Ocean (Anonymous, 1986). During the program 35 000 skipjack were tagged and released, approximately 30 000 in the eastern Atlantic and 5 000 in the western Atlantic as well as several thousand yellowfin and bigeye tuna. Both sonic tags and conventional tags were released on skipjack tuna (Anonymous, 1986). This program had many goals including understanding skipjack stock structure, spawning areas, migration, mortality, growth, recruitment and catch per unit effort (CPUE). Skipjack migration analyses were focused in the eastern Atlantic and were not quantitative.

In response to low yellowfin catches in 1983-1984, ICCAT initiated the Yellowfin Tuna Year Program (YFTYP) to tag yellowfin tuna and analyze growth patterns, fishing mortality, size composition of catch, and aging of hard parts (Anonymous, 1991). Three thousand yellowfin were tagged between 1986 and 1987 were tagged and only 138 were recovered. Approximately 400 large yellowfin tuna were tagged in the western Atlantic by US sport fishermen, the first time yellowfin larger than 100cm were tagged in the Atlantic. While too few tags were recovered to estimate

movement rates, researchers concluded that small yellowfin tuna did not make transatlantic movements while the large adult tuna did (Anonymous, 1991).

The most recent major tropical tuna tagging program from ICCAT is the Bigeye Tuna Year Program (BETYP) which tagged bigeye tuna, skipjack tuna, and yellowfin tuna from 1999-2003 (Fisch, 2005). During this program approximately 22 600 tuna were tagged in the Azores, Madeira, Canary Islands, Senegal, Ghana, São Tome, and Principe. Half of the tagged fish released were skipjack while yellowfin and bigeye tuna accounted for a quarter of the tags released. Almost 4 000 tags were recovered, with bigeye tuna having the largest recovery rate (31.3%), followed by skipjack (13%) and yellowfin (7.7%). During the BETYP 23 popup satellite tags (PSAT) and 19 data storage archival tags were also released (Fisch, 2005). PSAT data were used to estimate diving depth and duration, diel movements, and water temperature limitations. The program also collected DNA samples for stock structure analysis, data for growth studies, and injected tagged fish with antibiotics for validation of otolith aging studies. Hallier (2005) described movements obtained from tag releases and recovery data, however no quantitative analysis was performed.

The Mattes de thons Associées aux Canneurs (MAC) program was a program implemented by the French Institut de Recherche pour le Développement in 1996-2000 (Hallier and Delgado de Molina, 2000; Hallier, 2005). The tagging program focused on the associated school fishing technique based in the Dakar, Senegal baitboat fleet. During this program 10 000 fish were tagged: 3 000 bigeye, 6 700 skipjack, and 1 500 yellowfin. Approximately 3 000 fish were recovered, with the majority of the recoveries

bigeye tuna (57% recovery rate). The majority of the tag recoveries were within three months of release and few were outside the Senegal fishing area.

In general, these tagging programs have taken place on baitboats and they have been used to evaluate growth, fishing techniques, movement and migration (Gaertner *et al.*, 2006). While the majority of recoveries in the RTTP-IO were on purse seine vessels, over 50% of tags returned in the Atlantic have been on baitboats (Hallier, 2005). Most of the recoveries of yellowfin and skipjack tuna were within three years of their release; however bigeye tuna have been recaptured after longer times at liberty (Hallier, 2005).

Atlantic Ocean Tuna Tagging Program

A large scale tagging program has been implemented in the Atlantic Ocean (Atlantic Ocean Tuna Tagging Program or AOTTP) with tagging beginning in June 2016 in order to address some of the data gaps in the stock assessments (Anonymous, 2013). The success of this program will depend upon the combination of having an appropriate methodological design, successfully implementing this design in the field, and collaborating with the fishing industry to ensure the accurate reporting of tags (Die *et al.*, 2013). The chapters of this dissertation contributed to the improvement of the population dynamic models of the tropical tunas in the Atlantic and provided recommendations for the tagging operations of the AOTTP to ensure the program meets the stated goals. In order to provide recommendations to the AOTTP using a simulation study of the tagging program, models parameters were first estimated from tagging studies in the Atlantic, Indian, and Pacific Oceans. Then two important methodological design questions were asked: Which of the two electronic tags, pop-up satellite archival or data storage tags, will provide the best information on movement rates and how does

the plan to tag exclusively from baitboats impact the estimates of population wide parameters due to the size-selectivity of the different gears.

A spatially explicit simulation model was developed which was used to test the performance of current tagging design proposals to estimate parameters like fishing and natural mortality, conditional on the estimates of movement rates from electronic tagging. The chapters (i) investigated the success and results of historical tagging programs including large scale tagging programs in the Indian and Pacific Oceans as well as small scale tagging programs in the Atlantic Ocean; (ii) developed Bayesian priors for stock assessment parameters using tagging data from the Indian and Pacific Oceans; (iii) used data from historical tagging in the Atlantic Ocean to analyze the movements of tropical tunas; (iv) developed Bayesian priors for migration parameters for the tropical tunas in the Atlantic Ocean; (v) developed a spatially explicit model to investigate the impact of using two different kinds of electronic tags to provide movement rate priors for a conventional tagging model; and (vi) developed an age-structured spatially explicit simulation of a multi-species tagging operation to account for the size selectivity of fisheries involved in tagging and recapture programs and movement of tropical tunas into different regions and fisheries.

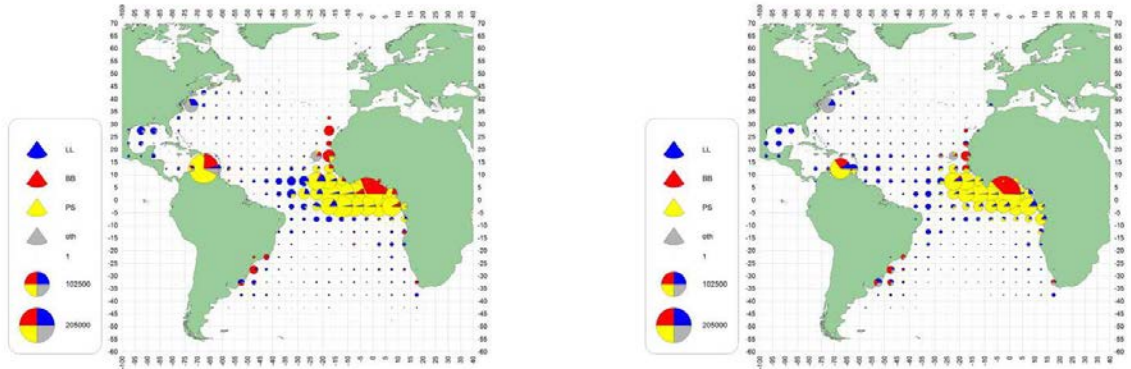


Figure 1.1. Cumulative Atlantic yellowfin tuna catches by gear from 1990-1999 (Left) and 2000-2009 (Right). Yellow indicates catch by purse seiners, red indicates catch by baitboats, blue indicates catch by longline, and gray indicates catch by other gears.

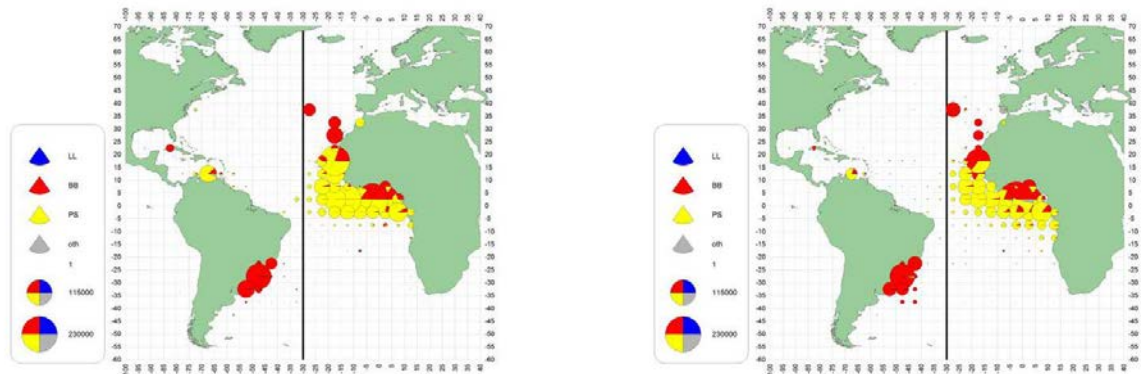


Figure 1.2. Cumulative Atlantic skipjack tuna catches by gear from 1990-1999 (left) and 2000-2009 (right). Yellow indicates catch by purse seiners, red indicates catch by baitboats, blue indicates catch by longline, and gray indicates catch by other gears.

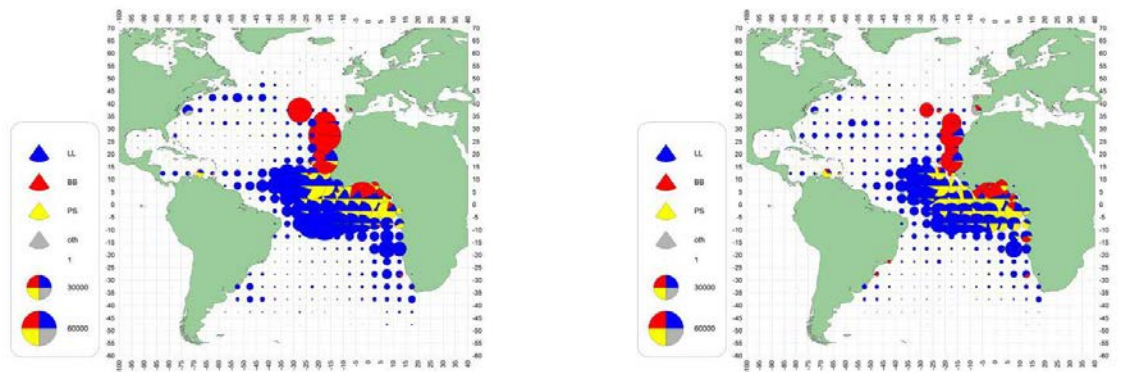


Figure 1.3. Cumulative Atlantic bigeye tuna catches by gear from 1990-1999 (left) and 2000-2009 (right). Yellow indicates catch by purse seiners, red indicates catch by baitboats, blue indicates catch by longline, and gray indicates catch by other gears.

CHAPTER 2: A BAYESIAN MODEL TO ESTIMATE MOVEMENT RATES FROM HISTORICAL TAGGING DATA AND CATCH PER UNIT EFFORT DATA FOR ATLANTIC TROPICAL TUNAS

Summary

Movement rates of Atlantic tropical tunas, *Thunnus obesus*, *T. albacares*, and *Katsuwonus pelamis*, were estimated using a spatially structured Bayesian tagging model informed by conventional tagging data from the International Commission for the Conservation of Atlantic Tuna (ICCAT) tagging database and relative abundance indices obtained by standardizing catch per unit effort data. Values estimated from previous studies in the Atlantic, Pacific, and Indian Oceans as well as recent stock assessments from ICCAT were used to develop informative lognormal priors for fishing mortality and informative beta priors for tag shedding rates and reporting rates. Natural mortality parameters were given highly informative priors with means equal to values used at the most recent ICCAT stock assessments. Movement rates were given uninformative dirichlet priors. Bayesian posterior movement parameters were estimated using a three region model of the entire Atlantic for yellowfin tuna and a six-region model of the Eastern Atlantic for skipjack tuna and bigeye tuna. Catch per unit effort data (CPUE) were standardized in each of the eight regions for each of the three species using a delta model. Migration parameters for yellowfin tuna showed less than 10% of the population within a region moving to a different region annually. Individual bigeye tuna move frequently between regions, with net northward movement between the Gulf of Guinea and northeast Atlantic as well as non-directional movement within the Gulf of Guinea. The movements between the Gulf of Guinea and the northeast Atlantic are likely seasonal as indicated by the high CPUEs in these areas in the spring and early summer and low

CPUEs in the winter. Annual residency rates were low for the majority of the eight regions, with only the Senegal and Canary Islands regions with residency rates greater than 0.5. Skipjack tuna net movement tends to be towards the northwest Atlantic, to the Canary Islands and Senegal regions which have residency rates >90%. Similar to bigeye tuna, there are some non-directional movements of skipjack tuna within the Gulf of Guinea, although in general annual movement rates are lower and annual residency rates are higher for this species than for bigeye tuna. The CPUE patterns of skipjack tuna are similar to bigeye tuna, although this species enters the northern regions a month or two after bigeye tuna. Yellowfin tuna move into these northern regions latest in the year, when the surface waters are warmest. This study is the first attempt to quantitatively estimate movement rates and the timing of the movement of tropical tunas. To improve the estimates of these movement rates additional tagging of these species in the Atlantic is necessary.

Background

Fishery assessments and the management strategies that they inform often make simple assumptions about fish movement. For tropical tunas a common assumption is that within the area of a fish stock, individual fish move in such a way that the location of where fish are harvested does not influence stock dynamics. If fish move in a different way, stock assessments may be biased and fishery management strategies may not perform as planned. The movement of tropical tunas, *Thunnus albacares*, *T. obesus*, and *Katsuwonus pelamis*, is poorly understood and probably complex. To understand such movement it is essential to first be able to observe or estimate movement of individual

fish, and second to understand how such movements relate to population abundance. While large numbers of tropical tunas have been tagged in the three major oceans, there is still large uncertainty in the magnitude and timing of these movements. Previous work has described movements of tropical tunas in the Atlantic, Pacific, and Indian Oceans; however, large-scale movement rates have not been estimated quantitatively. This work will focus on the movements of tropical tunas in the Atlantic Ocean, estimating movement rates using data from tagging programs implemented in the Atlantic but also informed by tagging data in the Pacific and Indian Oceans.

The majority of the research that has been undertaken on tropical tuna movements have been small scale projects involving pop-up satellite tags, archival tags, or acoustic tags and these studies are typically focused on movements of tunas around fish aggregating devices (FADs), or seamounts, or regional movement patterns (Holland *et al.*, 1990; Kleiber and Hampton, 1994; Dagorn *et al.*, 2000; Itano and Holland, 2000; Schaefer and Fuller, 2002; Musyl *et al.*, 2003; Girard *et al.*, 2004; Matsumoto *et al.*, 2005; Dagorn *et al.*, 2007; Schaefer *et al.*, 2007; Arrizabalaga *et al.*, 2008). Despite several large scale tagging programs for tropical tunas in the Pacific and Indian Oceans which have provided general descriptions of tropical tuna movement, movement rates have not yet been estimated (Fink and Bayliff, 1970; Williams, 1972; Fonteneau and Hallier, 2012; Motah *et al.*, 2012). However, these studies do provide estimates of tag shedding rates and reporting rates from fleets also found in the Atlantic which can be used to provide prior information for analyzing Atlantic Ocean tagging programs (Carruthers *et al.*, 2014). Historical tagging studies in the Atlantic Ocean have described bigeye tuna and yellowfin tuna movements along the African coast; however, these

studies were primarily regional and often did not record many tag recoveries outside of the region of interest, which makes them limited in their applicability to the Atlantic tropical tuna stocks (Miyabe and Bard, 1986; Sibert *et al.*, 1999; Hallier, 2005; Carruthers *et al.*, 2010). Studies in all three oceans describe a similar trend in movements for all three species: north and south movements seasonally, with limited east-west movements.

Movement information from tagging data is often hindered by the short time-at-liberty for tagged individuals. Tagging studies have shown that approximately 70% of tag returns for tropical tunas in the Atlantic are within 30 days of tagging, which does not permit the animal to make extensive movements (Anonymous, 2013). The movement information from these tagging studies have included time-at-liberty, total distance traveled, and general direction traveled but not estimates of the proportion of fish which move between regions in a year or season (Miyabe and Bard, 1986; Kleiber and Hampton, 1994; Hallier, 2003; Anonymous, 2013).

Catch per unit effort (CPUE) data is often used as a relative index of abundance of a population over time. Annual CPUE averages on a fleet by fleet basis can then be combined using a stock assessment model to give an estimate of abundance and stock status. Alternatively, CPUE data can be analyzed to provide a monthly relative index of abundance which, when combined with the annual movement rate estimates, could provide indications of the seasonal timing of the estimated movements (Fonteneau and Marcille, 1993). Additionally, the tagging data available are primarily representing juvenile tunas and including the CPUE indices will provide information on the movements of adult tuna. Using CPUE as a relative index of abundance can have many

pitfalls, including index hyperstability or hyperdepletion, and CPUE can be biased by changes in targeting strategy or fishing efficiency over time (Maunder and Punt, 2004; Maunder *et al.*, 2006; Carruthers *et al.*, 2010). For highly migratory species like tuna, where CPUE observations cannot always be obtained for the entire distribution of the stock often because of the expansion or contraction of the fishery over time, these indices need to be carefully calculated (Walters, 2003). However, aggregating multiple years together to look at patterns of abundance over the course of an average year may minimize many of these problems by averaging out the changes in the fishery over time. The relative change in CPUE over the course of a year should be constant even if the fishery changes significantly over the range of years analyzed, assuming that the fishery is relatively constant over the course of a single year. This method cannot differentiate between the arrival of new animals due to seasonal movements and the increase in CPUE due to recruitment; therefore indices in areas where recruitment occurs cannot be used to describe seasonal movement patterns.

Spatially explicit stock assessment models, including Stock Synthesis 3 (SS3), Integrated tagging and Catch at Age analysis (ITCAAN), migratory catch-age analysis, and MULTIFAN-CL all require parameters that describe the movement of the species between user-defined areas (Quinn, II *et al.*, 1990; Fournier *et al.*, 1998; Methot Jr and Wetzel, 2013; Goethel *et al.*, 2014). Due to the lack of such estimates, these models have seldom been used to assess the status of tropical tunas, although they have been shown to be useful in other species like sablefish, Pacific halibut, and albacore tuna (Quinn, II *et al.*, 1990; Heifetz and Fujioka, 1991; Aires-da-Silva *et al.*, 2009; Carruthers *et al.*, 2011; Goethel *et al.*, 2011; Goethel *et al.*, 2014).

Aires-da-Silva *et al.* (2009) and Stewart (2007) applied Bayesian models to estimate movements of Atlantic blue sharks and English sole, respectively (Hilborn, 1990; Xiao, 1996). Schirripa (2011) used SS3, and de Bruyn *et al.* (2011) used MULTIFAN CL, both statistically integrated assessment models, with a simple three-region structure that allowed the estimation of movement rates for Atlantic bigeye tuna. Both studies report that tagging data had some information on movement and spatial distribution, that influenced the assessment results, however, both also report that these data did not allow for precise estimates of movement rates across the spatial areas defined in their studies (Anonymous, 2011).

The objective of this paper was to adapt these Bayesian models to estimate annual movement rates of the three species of tropical tuna between regions in the Atlantic Ocean, using historical conventional tagging and CPUE data from the International Commission for the Conservation of Atlantic Tunas (ICCAT) database. CPUE data analyzed were from the ICCAT Task II catch/effort database from 1975-2005, the same time period from which the tagging data were collected (Anonymous, 2014d). The results of these Bayesian movement models and CPUE standardizations were annual movement rate estimates for all three species along with seasonal patterns of movements into the more temperate areas of their distribution.

Methods

Analysis of historical tagging data

Data

Tagging data were obtained from the ICCAT conventional tagging database for each species (Anonymous, 2014e; Anonymous, 2014c; Anonymous, 2014a). An initial analysis of the number of tags released each year was used to define release events for each of the species. The ranges of years analyzed in the models were chosen to correspond with known tagging programs as well as to ensure that there were enough tag returns in each year to estimate movement rates.

Bigeye tuna tagging data included in this analysis corresponded to fish released from 1993-2003 and recovered from 1993-2005, which equates to a recovery period of up to three years after release in the model. This results in 8 345 tags released and 2 159 tags recovered and included in the analysis. One tag recovery made 10 years after release was not included in the model because only three years of recovery were modeled; additionally, tags recovered within 30 days of release were not included in the model. Due to the distribution of tags released and recovered, and the limited number of transatlantic recoveries, a regional model of the eastern Atlantic was used to model the movements of bigeye. The area was divided into six regions which roughly correspond to the different fisheries and fleets which operate in the area based upon those proposed by Fonteneau *et al.* (2000a, **Figure 2.1a**). These regions also correspond to biologically important areas for bigeye tuna, areas where bigeye may feed, reproduce, or recruit. These regions also correspond to the highest catches of bigeye in the surface fisheries, where the majority of tagged fish are released and recovered (ICCAT, 2013).

Tagged yellowfin tuna were released from 1975 to 2003, corresponding to 17 309 tags released and 1 399 tags recovered included in the analysis. The model allowed for tags to be returned up to four years after their initial release, 1975-2007, which account for over 99.5% of the tags recovered during that time frame. Tags which were recorded as returned but did not have release location and/or recovery location or were recovered within the first 30 days of release were not included in this analysis. Due to the large numbers of tagged fish released in both the western and eastern Atlantic, a full-ocean model was deemed most appropriate (**Figure 2.1b**). The ocean was divided into three regions. Region one consists of the northeast Atlantic north of 7°N and east of 35°W. This region included the entire Azores fishery. Region two consists of the southeast Atlantic south of 7°N and east of 32°W. This region included the entire Gulf of Guinea and excludes the Brazilian fishing grounds. Region three included the entire western Atlantic not included in regions one and two. The Brazilian fishing grounds were combined with the Caribbean Sea and northwest Atlantic due to the limited number of tag releases and absence of tag recoveries in that area.

Tagged skipjack tuna were released from 1980 to 2002, with 37 503 tags released and 5 374 tags recovered included in the model. The model allowed for tagged fish to be returned for two years after the release event, 1980-2003, which accounted for 99.8% of the tag recovered. Only tags with complete recovery information (both date and latitude/longitude data) and tags from fish which were recovered more than 30 days after release were included in the movement model. Like the tagging data from bigeye tuna, the majority of tags were released in the eastern Atlantic (**Figure 2.1c**). Skipjack are believed to reproduce in the coastal areas of the Gulf of Guinea, then move into the

central gulf and Northwest African coast to feed (ICCAT, 2013). Ideally such movement behaviors should be reflected in the selection of regions for the skipjack model. The skipjack model uses the same six regions as the bigeye tuna model.

Model

A Bayesian model was used to fit the number of tags returned in each year and each region. The model consisted of three parts, a population dynamics model, an observational model, and the likelihood. The number of tags remaining in the population each year in each region was defined by the equation:

$$\mathbf{NTag}_{i,y+1,k} = \sum_{s=1}^n \mathbf{NTag}_{i,y,s} e^{-(M+\lambda+F_y)} \mathbf{m}_{s,k} \quad 2.1$$

where $\mathbf{NTag}_{i,y+1,s}$ was the number of tagged fish remaining from tagging group i , in year $y+1$, in region s ; M was natural mortality, λ was the type II tag shedding which accounts for the long term tag loss, F_y was the total fishing mortality for year y ; and $\mathbf{m}_{s,k}$ was the movement rate from region s to region k . Natural mortality, fishing mortality, and tag shedding were all instantaneous rates across the year. Movements were assumed to occur once, at the beginning of each year before mortality occurs. The model allowed fish to move into other regions in the first year, thus the number of tagged fish in the first year was $\mathbf{NTag}_{i,y,k} = T_i * \mathbf{m}_{s,k}$, where T_i was the number of tags released in tagging group and the movement m from the release region s to region k occurs immediately after the tags were released. The expected number of tags caught in each year and region was estimated using a Baranov catch equation:

$$\mathbf{TR}_{i,y,k} = \left(\frac{F_y}{M + \lambda + F_y} \right) \mathbf{Ntag}_{i,y,k} (1 - e^{-(M+\lambda+F_y)}) R_k \quad 2.2$$

where $TR_{i,y,k}$ was the expected number of tag returns from tagging group i , in year y , in region k , and R_k was the reporting rate in region k .

Informative priors were used for tag shedding, reporting rates, and fishing mortality (**Table 2.1**). Priors for type II tag shedding (instantaneous, long term tag loss) were defined as beta distributions for each of the three species separately with means and standard deviations equal to the mean of the tag shedding parameters previously estimated in tagging programs throughout the Atlantic, Pacific, and Indian Ocean for each species, and the standard deviation of those means (Bayliff and Mobrand, 1972; Kleiber *et al.*, 1987; Hampton, 1997; Adam and Kirkwood, 2001; Gaertner and Hallier, 2004; Gaertner and Hallier, 2008). Priors for reporting rates for each species in each region were developed from previous tagging studies including the Atlantic Bigeye Tuna Year Program (BETYP, Carruthers and McAllister, 2010; Carruthers *et al.*, 2014) and the Indian Ocean Region Tuna Tagging Program (IO-RTTP). These reporting rate priors were developed by identifying the fleets which target tropical tuna in the Atlantic and assigning them a reporting rate. A fleet's reporting rate was equal to the previously estimated reporting rate in the Atlantic or Indian Ocean tagging programs, for example the Japanese Longline or European purse seiners have previously estimated reporting rates. If there are no previously estimated reporting rates for a fleet, the mean reporting rate across all Oceans for that gear was used. Reporting rate priors were estimated for each region and species. The prior mean reporting rate in each region was calculated as the mean of reporting rates for each gear and fleet combination weighted by its contribution to the total catch in each area. The catch of each region by fleet and gear was compiled from the last 20 years of ICCAT Task II catch and effort data (Anonymous, 2014d). For those

fleets without previous reporting rate estimates, the mean reporting rate for the gear was used. The standard error of the reporting rate priors was the square root of the weighted variance of the mean reporting rates for each region and species. In some runs, reporting rates were fixed at the prior mean value.

Fishing mortality (F) priors were developed using estimated fishing mortality from ASPIC or Bayesian Surplus Production (BSP) models in previous stock assessments for each of the species. Fishing mortality parameters were given a lognormal prior with the mean and variance set to the mean fishing mortality across all available ASPIC runs for each species from the most recent stock assessment and the variance of those means. Two hypotheses on fishing mortality were tested for yellowfin tuna, one in which F was constant throughout the entire period, and one which estimated a fishing mortality in five year increments, reflecting the dynamic nature of the surface fisheries catching these species. This allowed the fishing mortality to increase with the increase in FAD fishing over time, which is presumed to have caused an increase in catchability by the purse seine and baitboat fleets (Fonteneau *et al.*, 2000b). Fishing mortality was assumed to be constant for bigeye tuna over the entire time period because all the data were post-1990, which corresponds to the start of significant fishing on FADs (Fonteneau *et al.*, 2013). Skipjack fishing mortality was separated into two time periods, from 1980-1990 and post-1990. Uninformative dirichlet priors were used for movement rates, so that the number of parameters estimated is equal to the number of regions minus 1, due to the constraint $\sum_1^k m_{s,k} = 1$. It was assumed that there was no movement out of the regions of interest, although this might not be a realistic assumption for BET and SKJ.

Natural mortality was given a highly informative prior due to the difficulty of estimating natural mortality, fishing mortality, and movement rates from a single source of data. The means of these priors were the natural mortalities assumed in the most recent ICCAT stock assessments, 0.8 for juvenile bigeye tuna (Anonymous, 2016b), 0.8 for skipjack tuna (Anonymous, 2014b), and 0.7 for juvenile yellowfin tuna (Anonymous, 2011). All priors were assumed to have a coefficient of variation equal to 0.01.

A negative binomial likelihood was used; the over dispersion allowed by this likelihood represents the propensity for tunas to school (Michielsens *et al.*, 2006). The probability density function of the data x given the number of events, r and the probability of success, p was:

$$p(x_{i,y,k}|r, p_{i,y,k}) = \frac{\Gamma(r + x_{i,y,k})p_{i,y,k}^r(1 - p_{i,y,k})^{x_{i,y,k}}}{\Gamma(r)\Gamma(x_{i,y,k} + 1)} \quad 2.3$$

where $x_{i,y,k}$ was the number of tags returned from tagging group i , year y , region k , r was the additional variance parameter, which had an uninformative gamma prior, and $p_{i,y,k}$ was calculated as $r/(r+TR_{i,y,k})$ for tagging group i , year k , region k .

Each model was run in JAGS 3.4.0 (Plummer, 2003) via R 2.15.2 (R Computing Team, 2014) for at least 500,000 Monte Carlo Markov Chain (MCMC) iterations with a burn in of 50,000 iterations with a thin of 10 or until convergence was reached. The convergence of the MCMC to the stationary posterior distribution was evaluated by the Gelman-Rubin diagnostic, based on the ratio of inter-chain variance to intra-chain variance (Gelman and Rubin, 1992) as well as evaluating the trace plots of each estimated parameter. Model fit was evaluated with a Bayesian P value, which measures

the discrepancy between the observed data and the assumed model using simulated replicated data (Lunn *et. al*, 2013).

CPUE Standardization

Catch per unit effort was extracted from Task II catch and effort data for each species in each of the eight regions of interest between 1975 and 2005 (Anonymous, 2014d). This database provides catch and effort data aggregated by month, year, fleet, effort type, and 5x5 degree square for all of the species monitored by ICCAT. These regions are the same as those used for the bigeye tuna model with the addition of the Azores region and the separation of the North Sherbro region into the Sherbro and North Sherbro region (**Figure 2.2**), are used for all three species in the CPUE standardization to explore movement rates in the Eastern Atlantic Ocean, and are the regions in which the majority of the tropical tuna catch occurs. The database was filtered such that reported effort was included in the analysis if at least one of the three species were captured in a record. This method was used to identify effort targeting the tropical tunas or catching them as bycatch and eliminate effort, primarily longline effort, which targeted one of the other species ICCAT manages. The majority of the records removed corresponded to longline fleets which likely were targeting swordfish or albacore in the eight regions of interest. The final dataset analyzed consisted of over 75,000 entries with 30% of the bigeye entries zero catch, 25% of the yellowfin tuna entries zero catch, and 11% of the skipjack tuna entries zero catch. Therefore, a delta model was used to analyze the proportion positive and positive only catch and effort data records from the filtered ICCAT database (Lo *et al.*, 1992).

Positive catches in each region were standardized using a generalized linear model of the log-transformed CPUE using a Gaussian density distribution and an identity link function with up to five explanatory categorical variables: year, month, type of effort, flag, and gear (**Table 2.2**). No interactions were included in the model. Year and month are factors with 23 and 12 levels, respectively. Fleet is a factor with 35 levels, representing each of the flags which fish for tropical tunas in the Eastern Atlantic. Gear is a factor with three levels: purse seine, baitboat, and longline. Type of effort is a factor with 11 levels; these levels represent the different units of effort that are reported to ICCAT which are not always consistent within a gear or a fleet. For example, purse seine effort is reported as days at sea, fishing hours, fishing days, etc., and causes the scale of the CPUE to vary from <1 to thousands of kilograms per unit effort. Inclusion of this factor allowed us to account for the large variability in scale within the CPUE data which was not due to changes in abundance. The proportion positive data were analyzed using a generalized linear model using a binomial density distribution and a logit link function.

A stepwise regression was used to determine the most parsimonious binomial and lognormal models for each region based upon the lowest Akaike Information Criterion (AIC) value and the number of factors included (Akaike, 1973). In some cases the model with the lowest AIC included a variable which had too few observations to allow for an estimate of the least squares mean, in this case, the CPUE model with the lowest AIC which excluded this parameter was used to standardize the data. Generally these alternative CPUE models had ΔAIC values less than 5, which indicated that the

alternative model has good support for being the most parsimonious model and allows us to make the substitution with confidence that the results will not be impacted (McCarthy, 2007).

In total, 13 models were evaluated for use (**Table 2.2**). The least square means are the means estimated from a linear model, they are adjusted to other terms in the model and which balances out the unequal number of observations in each factor level. They are less sensitive to missing data, making their use in CPUE standardization valuable (Searle *et al.*, 1979). Least square means were estimated for the month factor, which accounted for the other factors included in the model. They were transformed back into natural scale using the lognormal bias correction factor for the positives only model and the binomial transformation for the proportion positives model. Monthly standardized CPUE was then obtained as the product, in natural scale, of the least square means of the proportion positives and the least square means of the positives.

Results

Historical tagging data analysis

Parameter Estimates

All three movement models had difficulty estimating reporting rates along with fishing mortality and natural mortality. When reporting rates were estimated, the region(s) with the fewest returns had an estimated reporting rate of zero and the model estimated large movement rates into that region thus predicting that none of them were recovered because of the low reporting. Since there were tags recovered in every region, it is unlikely that reporting rates were zero in any region and we can assume that

movement estimates from these models are unlikely to be accurate. The conventional tagging data did not contain enough information to estimate both movement rates and reporting rates. Unfortunately very little information on the reporting rates for each release event included in the models was available. When the mean of the prior was used as the fixed reporting rate, the movements were estimated with more precision (due to fewer parameters to estimate) and the estimates were likely to be a more accurate reflection of the information contained in the data. Therefore fixed reporting rates were the best method to estimate movement rates with the data currently available. All models reported in the following used fixed reporting rates.

The model selection criteria for yellowfin and skipjack preferred the movement models with a single fishing mortality; therefore results presented will be for the single fishing mortality estimate (**Table 2.3**). The movement models estimated similar fishing mortalities to those estimated in recent stock assessments for all three species in part because of the informative priors. For bigeye fishing mortality the posterior mean was 0.25 (CV=0.09, Appendix A), skipjack mean was estimated to be 0.1 (CV=0.01, Appendix A), and yellowfin mean fishing mortality was around 0.17 (CV=0.17, Appendix A). Tag shedding rates were low for bigeye tuna but poorly estimated (0.1, CV=1.82). Tag shedding for skipjack and yellowfin tuna were better estimated but very high compared to previous estimates of shedding: 0.79 (CV=0.12) for skipjack and 0.39 (CV=0.19) for yellowfin (Gaertner & Hallier, 2008, Adam & Kirkwoor, 2001, Kleiber *et al.*, 1987, Gaertner & Hallier, 2004, Hampton, 1997, Bayliff & Mobrand, 1972).

Bigeye tuna

Overall the movement model fitted the data well with a Bayesian p-value = 0.49; however it tended to underestimate annual tag returns (**Figure 2.3**) with residuals generally negative or around zero (**Figure 2.4** and Appendix A). Movement rate estimates suggested that there is a lot of exchange between the Gulf of Guinea and the north-east Atlantic although this appeared to be generally a northward movement of animals with much lower movement rates from the north to the Gulf of Guinea (Azores/Canary Islands, **Figure 2.5**). Fish appeared to move between regions frequently within the Gulf of Guinea, with residency rates <0.5 in all the regions. There were high residency rates in the Canary Islands and Senegal paired with movement rates $>10\%$ into those regions from many of the other regions. The Azores had a very low residency rate, with only 11% (CV=0.91) of the fish released in the Azores recaptured in the Azores in subsequent years. These movement rates, however, do not appear to be well estimated, with the majority of CVs $>50\%$ and even some $>100\%$.

Yellowfin tuna

In general, both yellowfin movement models fitted the data fairly well with Bayesian p-values of 0.7 and 0.71 for the single F and multiple F models, respectively. Model diagnostics preferred the movement model with a single fishing mortality over the one with multiple fishing mortalities, although the Δ DIC was fairly small, only 6.4 (**Table 2.3**). The movement model generally overestimated returns except for the beginning of the time series when returns were generally underestimated (**Figures 2.3 and 2.4**).

Yellowfin tuna appeared to have very high residency rates in each of the three regions (>90%). Movement rates from west to east were around 10% whereas movement rates from east to west were around 2%, while north and south movements between regions one and two appeared to be relatively equal (0.06 CV=0.52 and 0.08 CV=0.46, **Figure 2.5**). Movement rates for yellowfin tuna were much better estimated than bigeye tuna, with the majority of the CV values <0.5 and only one equal to 100%.

Skipjack tuna

Both skipjack movement models fitted the data somewhat poorly with the Bayesian p-value =0.8 for both but, model diagnostics preferred the movement model which estimated a single fishing mortality over two fishing mortalities (**Table 2.4**). The movement model fitted years with few tag returns between the two large tag release events well (**Figure 2.3**), but generally overestimated the number of tags returned when there are large tag release events, with large positive residuals (**Figure 2.4**). The movement estimated from the model suggested a net northward movement from the Gulf of Guinea to northwest Africa, although the majority of this movement comes from the more western regions and not from the primarily coastal regions of Cote d'Ivoire and Cape Lopez (**Figure 2.5**). Both the Canary Islands and Senegal had very high residency rates, 0.98 (CV=0.01) and 0.92 (CV=0.02), respectively. The regions within the Gulf of Guinea had lower residency rates, excepting Cote d'Ivoire, which had a residency rate of 0.86 (CV=0.04). The movement rates within the Gulf of Guinea tended to be towards the north or into the Equatorial and Cape Lopez regions. There was significant exchange between the Cape Lopez and Equatorial regions.

CPUE Standardization

Model fitting

The best lognormal and binomial model for many of the regions was the full model, including all five variables and an intercept, although in over half of the regions reduced models were the most parsimonious or were alternative models with a ΔAIC of less than 5 (Appendix A). Some CPUE models dropped year as an explanatory variable, which would not be recommended if the purpose of the standardization was to evaluate trends over time (Maunder and Punt, 2004). However, the interest here was the monthly trend, so year was allowed to be dropped if it was not statistically significant. Year was dropped for eight of the CPUE models, which supports the assumption that the seasonal trend in CPUE is stable over the time period analyzed. Since year did not explain a significant amount of the variability of the CPUE data for several of the regions, this justified the aggregation of years in the analysis for description of the monthly movement patterns. Model diagnostics and standardized monthly CPUE for all the three species in each of the eight regions can be found in Appendix A. In general all the models fit the data well.

Bigeye tuna

There were clear trends in monthly CPUE in the more temperate regions evaluated. In the Azores, bigeye tuna were primarily caught in April through July, with CPUE peaking in June. There were small catches in November and December, but no catch at all in January and February (**Figure 2.6**). In the Canary Islands, there was some catch year round, but the primary fishing season was in March – June with a peak in May. In Senegal/Cape Verde Islands, there were larger catches in July – February.

CPUE peaks in October and was at a minimum in May. For the other four regions, catches were fairly constant throughout the year, with no trends in the CPUE. There is significant variability in the catches during the peak seasons in the Azores and Canary Islands, although the general trend of increased CPUE during these periods is clear (Appendix A).

Yellowfin tuna

Trends in CPUE for yellowfin tuna were much less pronounced than for skipjack and bigeye. There was not a lot of CPUE data in the Azores, although catches tended to peak in September. In the Canary Islands, catches were larger in June through December with a peak in September (**Figure 2.6**). There were very low CPUE values in March through May. In Senegal, there was a slight increase in CPUE in July through December with a peak in September and October. For the other four regions, there was very little change in CPUE over the course of a year.

Skipjack tuna

Skipjack tuna CPUE also appeared to have seasonal trends in the more temperate regions, but trends were present in more regions than for bigeye (**Figure 2.6**). In the Azores, catches peaked in August but were elevated from June through November. Catches were very low (or zero) in December-May. In the Canary Islands, skipjack were caught primarily in June through December. CPUE peaked in July and August, with lower catches January through May and a minimum in March. CPUE peaked in Senegal in May through June but was higher between April and October. Generally CPUE was constant in November through March. In North Sherbro, there was a general increase in CPUE over the course of the year, peaking in October and then decreasing to a minimum

in February. CPUE peaked in December and January in Sherbro, with a minimum in March and peaks in April in Cote d'Ivoire and was relatively constant throughout the rest of the year. There were no significant trends in CPUE in Cape Lopez and the Equatorial regions.

Discussion

Short term recoveries of tagged animals pose a challenge for tagging models as they can bias parameter estimates by violating the assumption that the tagged population is fully mixed with the untagged population (Hoenig *et al.*, 1998). Short term recaptures can both positively bias fishing mortality and negatively bias movement rates. These animals can be modeled using a non-mixed model to calculate separate fishing mortalities for newly tagged animals and previously tagged animals. However, this method can be computationally intensive and can result in significantly increased standard errors (Hoenig *et al.*, 1998). Another method of accounting for “trap-happy” individuals in a multiple capture-recapture program is to remove the first recovery event for the animals and calculate parameters for the subsequent recaptures or model the animals which are recaptured separately from those that are not recaptured. Tags in this study are recovered at most once, however, they can be treated similarly to the “trap-happy” animals. Simulations by McGarvey and Matthews (2012) showed that when there is a single recapture event but many short-term recaptures, removing the early recaptures within the first few weeks of the study has very little impact of the estimate of total mortality precision and it can alleviate bias in the estimate of fishing mortality for the whole population. Therefore, the removal of the tags recaptured within 30 days of their release

will not likely bias the estimates of fishing mortality since natural mortality has a highly informative prior and will allow for unbiased estimates of movement rates.

Bigeye tuna

Previous research has suggested bigeye tuna make more north-south movements in the Atlantic Ocean than east-west movements. The current assumption about bigeye movements is that they are found north of Mauritania in July, with some fish continuing north towards the Canary Islands. From November to December bigeye tuna migrate south to the Gulf of Guinea. There they remain until March-April when they return north to the Senegal fishing grounds (Hallier, 2005). The large movement rates between the regions within the Gulf of Guinea and the northeast Atlantic estimated in the model are consistent with these previous descriptions of bigeye movements. Although the southern movements in November and December are not captured through the annual movement models, they are suggested by the CPUE models possibly because of larger numbers of tagged fish released in the Gulf of Guinea or due to high fishing mortality on fish tagged in the northern regions, which may be captured before they move, or are recaptured in the same region in the following year. The corresponding increases in the equatorial waters are likely confounded with recruitment signals. Furthermore, Carruthers *et al.* (2010) and Hallier *et al.* (2004) proposed that bigeye tuna move north and south along the North African coast and are generally dispersed throughout the Gulf of Guinea, a pattern that is seen in the low residency rates in the Gulf of Guinea regions and relatively equal exchange rates between them.

The CPUE data are consistent with the descriptions of movement from the tagging model. The CPUE data show the timing of the movement of bigeye into and out

of the northern regions. Based upon the CPUE data, bigeye tuna take advantage of their ability to withstand colder temperatures than skipjack and yellowfin and travel into the northern most regions first (**Figure 2.7**, Brill *et al.*, 2005). They appear to leave Senegal and the more southern regions in March, peak in May in the Canary Islands and reach the Azores in large numbers by June. They leave the Azores by August. They are caught in relatively large numbers during the rest of the year in Senegal. The movements back south into the Gulf of Guinea occur in the fall, September-November, and they likely winter in the warmer tropical waters before returning north in the spring. These movements may be linked to prey competition between the tropical tunas.

Yellowfin tuna

Yellowfin tuna movements are perhaps the best understood among the tropical tunas as they have been tagged in greater numbers and for a longer time period than either skipjack or bigeye tunas. The capture of fish in the west which had been tagged in the east and vice versa confirms significant transatlantic movements undertaken by these fish. Model estimates derived from tagging data analyzed here do not reflect those movements, with very small movement rates between the three regions. Movements north and south of the equator are limited but the exchange is fairly equal, as indicated by small movement rates between regions one and two. These results do not support the movement patterns proposed by Zagaglia *et al.* (2004) and Carruthers *et al.* (2010) for yellowfin tuna.

The movement model does estimate that approximately 9% (CV=0.33) of the fish tagged in the western Atlantic move to the eastern Atlantic, which is smaller than expected given that there are a number of tags recovered in the east which were tagged in

the west. Yellowfin are believed to concentrate in the eastern Atlantic between January and March for spawning followed by a transatlantic migration from east to west between March and May for spawning in June through September. The fish return to the eastern Atlantic between October and December (Zagaglia *et al.*, 2004). This would suggest much larger east-west movement rates than those estimated in the model. The annual estimates of movement rates may not capture the east to west and west to east movements that may occur within a single year, interpreting it as a high residency rate when fish released in a region are recaptured in that region in subsequent years.

There are two possible explanations for this discrepancy: first, there is insufficient data to estimate seasonal movement rates from the model and second, the majority of tagged fish are juveniles which do not make transatlantic movements for spawning. To make unbiased estimates of seasonal movement rates, tagging efforts should be evenly distributed throughout the year. However, the historical tagging events are concentrated in the summer months, with 80% of the tags released in quarters two and three. The majority of the tags that were recovered after a transatlantic migration were captured four or more years after they had been released. The movements described by Zagaglia *et al.* (2004) and Carruthers *et al.* (2010) are for the breeding population of yellowfin, but the majority of the tagged population are small juvenile yellowfin tuna. Yellowfin tuna mature around two years old and are believed to make their first transatlantic trip around age three. Since the majority of the tags recovered are within the first two years, tagged fish may be being recaptured before they have a chance to make these movements (Zagaglia *et al.*, 2004).

This delay in transatlantic movements by tagged yellowfin tuna suggests that recovery operations must be maintained for many years after tagging in order to obtain long distance recoveries. In general, recovery efforts, such as publicity campaigns and rewards for tag returns, are not maintained for more than a few years after the final tagging event, primarily due to the lack of funding appropriated to such efforts compared to tagging (Million, 2013). Furthermore, the few tags released in the Southwest Atlantic (<10) and the lack of tag recoveries in this region prevent us from making any conclusions about movements of yellowfin from that area. Additional tagging is required before this movement model can be used for a four region seasonal model of the Atlantic.

The CPUE data were analyzed to investigate movements north and south along the North African Coast from the Gulf of Guinea, which will give insights on movements between regions one and two in the Bayesian model, but also smaller scale movements of yellowfin. Yellowfin tuna are rarely caught in the Azores as their waters are likely too cold and these fish tend to be more tropical than skipjack or bigeye tuna and remain in waters warmer than 24°C (Brill and Lutcavage, 2001). However, they are caught in small numbers in the boreal fall. Yellowfin tuna appear to take advantage of the warmer surface waters in the Canary Islands in the boreal summer and fall, with catches peaking in September and October, before returning further south to the Senegal area and beyond, where CPUEs are generally constant and water temperatures are greater than 24°C throughout the year. They are not caught at all in these northern regions in February through May, suggesting they have left the Azores and Canary Islands in the coldest months. The CPUE results suggest that more movement between region one (Canary Islands, Azores, and Senegal) and region two (Gulf of Guinea) occurs than is captured in

the tagging data. This indicates the CPUE data is useful in providing additional information on the seasonal north and south movements of yellowfin tuna which is unavailable from the limited tagging data.

Skipjack tuna

A previous tagging study in Senegal and Mauritania concluded that most skipjack tuna movements are local and they remain in the fishing area with north and south movements along the northwest African coast (Miyabe and Bard, 1986; Hallier, 2005). Fish which were tagged in the Gulf of Guinea were found to have relatively dispersed movements westward from the Cote d'Ivoire and Cape Lopez regions. The movement rates estimated in this model supports some of these descriptions of tuna movement, with large residency rates in the northwest regions and movement between into the Equatorial region from other Gulf of Guinea regions and significant exchanges with Cape Lopez. This model also shows significant movement from the Gulf of Guinea to the Canary Islands and Senegal regions. The large residency rate in the Cote d'Ivoire may be reflective of a large fishing mortality in the area, where many of the fish are captured before they have the chance to move. This region is known to be an important spawning ground for all three species and has a FAD fishery with large catches (Fonteneau and Marcille, 1993). The high residency rate for skipjack in this region may also be due to the recapture of skipjack returning to the region for spawning which were tagged and released during previous spawning events.

The movement model cannot differentiate between fish remaining in the area throughout the year and fish returning to an area annually but moving between regions throughout the year. The current tagging data available are not informative enough to

make the movement model time steps seasonal rather than annual; 92% of the tags released for skipjack tuna are in the second and third quarters of the year, therefore there are not enough tag releases in quarters one and four to inform seasonal movement rate estimates. However, the CPUE data can give us information of the seasonal movements of skipjack. Skipjack tuna movements from CPUE data are similar to bigeye, although offset by a month or two. Skipjack tuna appear to travel north from the equatorial areas and peak in May-June in Senegal, followed by July and August in the Canary Islands, and some skipjack appear to continue north to the Azores in the boreal fall, peaking in August-October. These results suggest that the high residency rates in the Canary Islands and Senegal are most likely due to fish returning to the region each year, and not due to large numbers of fish remaining in the regions year round.

The lack of tagging data for the first and fourth quarters of the year could have management implications for the equatorial regions where the CPUE data is not sufficient to evaluate trends in the residency of bigeye tuna. ICCAT has recently expanded the moratorium on fishing on FADs in the Gulf of Guinea to extend from 5°N to 4°S and from the coast of Africa to 20°W in January and February (Anonymous, 2016d). This moratorium is an effort to reduce the catch of juvenile bigeye tuna, and the movement trends described above suggest that bigeye tuna do concentrate in the Gulf of Guinea during the first quarter. However, the tagging database does not contain enough information to confirm this residency. Of the 3 300 tags released on bigeye tuna in the moratorium region, only two were released in January and none in February. Only 27 tags were recovered in the region during January and February. This lack of returns could be due to reduced fishing effort during this time of the year; however the FAD

moratorium was implemented after the end of the current study. A concentrated effort to tag fish in this region during the first quarter of the year would be necessary to determine how effective this moratorium is at reducing juvenile bigeye tuna catch.

Conclusions

Movement rates estimated here generally agree with previously described movement patterns of tropical tuna in the Atlantic. Most of the movement rates have large coefficients of variation, likely due to the small recovery rates for the three species. Bigeye tuna are known to be better adapted for colder water temperatures, therefore it is not surprising that they reach the northernmost regions first, followed by a month or two by skipjack, and then yellowfin reaching the northern most waters when they are at their warmest (**Figure 2.6**, Graham, 1974; Brill, 1994). This pattern is clearly evident in the trends in CPUE between the three more temperate regions, the Azores, the Canary Islands, and Senegal. Juvenile bigeye tuna are believed to have prey preferences which overlap with similar sized yellowfin and skipjack tuna, targeting *Vinciguerria numbaria* in the Gulf of Guinea (Menard and Marchal, 2003) while also being fairly opportunistic in their prey choices (Lebourges-Dhaussy *et al.*, 2000; Menard *et al.*, 2006). However, adult bigeye tuna feed near the deep scattering layer, much deeper in the water column than the other two tropical species (Vaske *et al.*, 2012). It is believed that their movements are driven by the opportunity to feed in the more temperate regions where greater numbers of prey species are available as the water temperatures increase to those tolerated by the tropical tunas (Brill, 1994). Additional tagging efforts on these species will be valuable in estimating movement rates more precisely as well as additional studies on the seasonal distribution of their prey species.

The addition of catch and effort data to the tag-recapture model would likely also increase the accuracy of the movement estimates (Goethel *et al.*, 2014). These data were not included in this analysis due to several years of missing data in the ICCAT Task II database in some of the regions, specifically the Azores Islands and Canary Islands regions, in the 1990s. Due to the CPUE data being aggregated over a large time period, these missing data are unlikely to impact the seasonal patterns observed from the CPUE data; however it does prevent these data from being incorporated into the Bayesian model to estimate fishing mortality.

In this study, the large-scale annual movements of Atlantic tropical tunas from tagging data are estimated quantitatively for the first time and combined with standardized CPUE data to describe the seasonality of these movements. The Bayesian framework applied to the tagging data shows that movements of tropical tunas both throughout the entire Atlantic as well as between smaller areas in the eastern Atlantic can be estimated well with enough data. The results presented here provide an estimate of annual movement rates, residency rates, and the timing of seasonal movements in the temperate limits of their distribution. The combination of the CPUE data provide information on the timing of the movement rates estimated from the annual movement model in the temperate regions of their distribution while the movement model allows us to estimate annual movements in the tropical regions where movement and recruitment are confounded in the CPUE data. They corroborate previously hypothesized movement patterns for skipjack and bigeye, although some discrepancy remains with previous studies on yellowfin tuna. These results show significant exchange between regions within the Atlantic and suggest the need for spatially explicit stock assessment methods

into which these results can be incorporated and provide better estimates of the current stock status. Finally, the large uncertainty that remains around many of the movement rate estimates indicates a clear need for additional tagging data for all three species as well as more specific information recorded for the tagging program, including tag shedding estimates and reporting rates, and more extended recovery efforts to ensure the transatlantic movements are captured adequately. It is encouraging to know that such studies are being conducted as part of the ICCAT Tropical Tuna tagging program which started in 2016 (Anonymous, 2016a).

Table 2.1. Mean and standard deviation of tagging model priors.

Variable	BET		YFT		SKJ		Distribution
	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation	
Fishing mortality	0.22	0.07	0.21	0.09	0.1/ 0.15	0.01	Lognormal
Natural Mortality	0.8	0.004	0.7	0.007	0.8	0.008	Lognormal
Reporting Rate							Beta
Region 1 (NE)	--	--	0.32	0.33	--	--	
Region 2 (SE)	--	--	0.45	0.36	--	--	
Region 3 (W)	--	--	0.34	0.29	--	--	
Azores	0.21	0.24	--	--	--	--	
Canary Islands	0.09	0.19	--	--	0.06	0.19	
Cape Lope	0.32	0.32	--	--	0.29	0.30	
Cote d'Ivoire	0.31	0.26	--	--	0.26	0.26	
Equator	0.29	0.25	--	--	0.30	0.29	
N Sherbro	0.31	0.26	--	--	0.34	0.32	
Senegal	0.23	0.23	--	--	0.29	0.27	
Sherbro	0.36	0.29	--	--	0.38	0.33	
Tag Shedding	0.08	0.13	0.15	0.13	0.09	0.08	
Negative Binomial Variance	10	100	10	100	10	100	Gamma

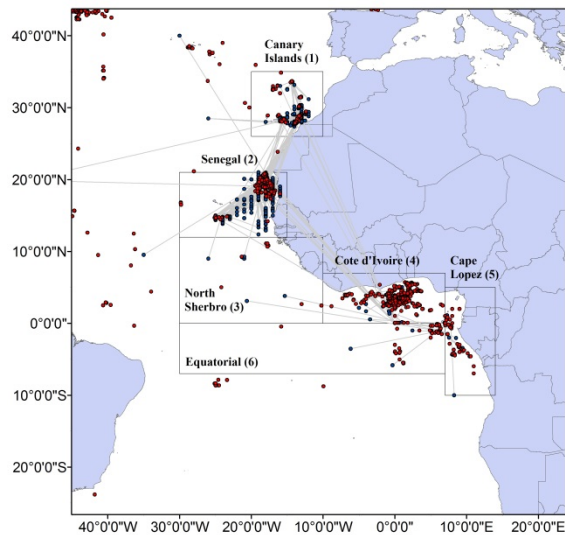
Table 2.2. List of Generalized Linear Models which were tested for $\log(\text{CPUE})$ and the proportion positive in each region and species.

Model	Explanatory Variables
1	Month
2	Month + Effort
3	Month + Effort + Fleet
4	Month + Fleet
5	Month + Gear
6	Year + Month
7	Year + Month + Effort
8	Year + Month + Gear
9	Year + Month + Fleet
10	Year + Month + Effort + Fleet
11	Year + Month + Effort + Gear
12	Year + Month + Fleet + Gear
Full	Year + Month + Effort + Gear + Fleet

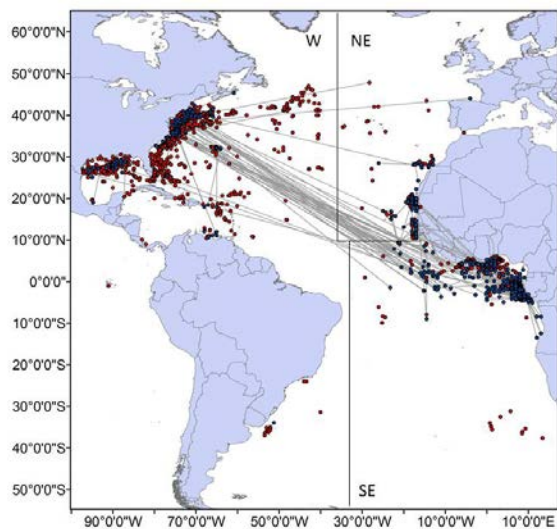
Table 2.3. Model Selection Criteria for skipjack and yellowfin tuna to evaluate the model improvement if they were permitted to estimate different fishing mortalities for different time periods.

Model	ΔDIC
SKJ - Single F	0
SKJ - Multiple Fs	54
YFT - Single F	0
YFT - Multiple Fs	6.4

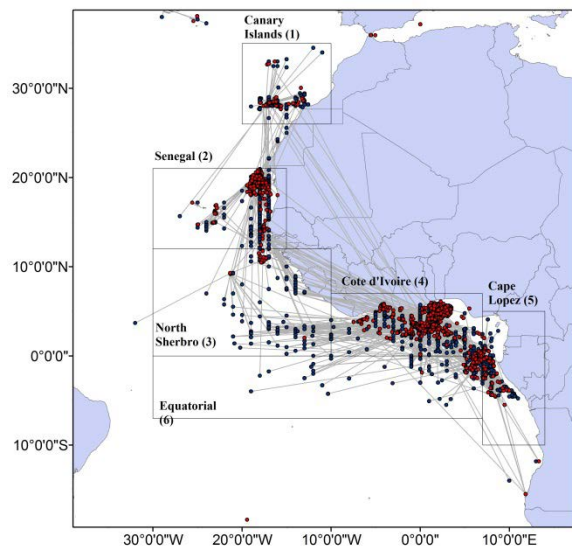
Figure 2.1. Maps of the fishing regions in the eastern Atlantic Ocean modeled for each species with tag releases (blue dots) and recoveries (red dots) and tracks of recovered fish (gray lines), and region names with corresponding numbers in parentheses: a.) The six region model for bigeye tuna; b.) The three region model for yellowfin tuna; c.) The six region model for skipjack tuna.



a.



b.



c.

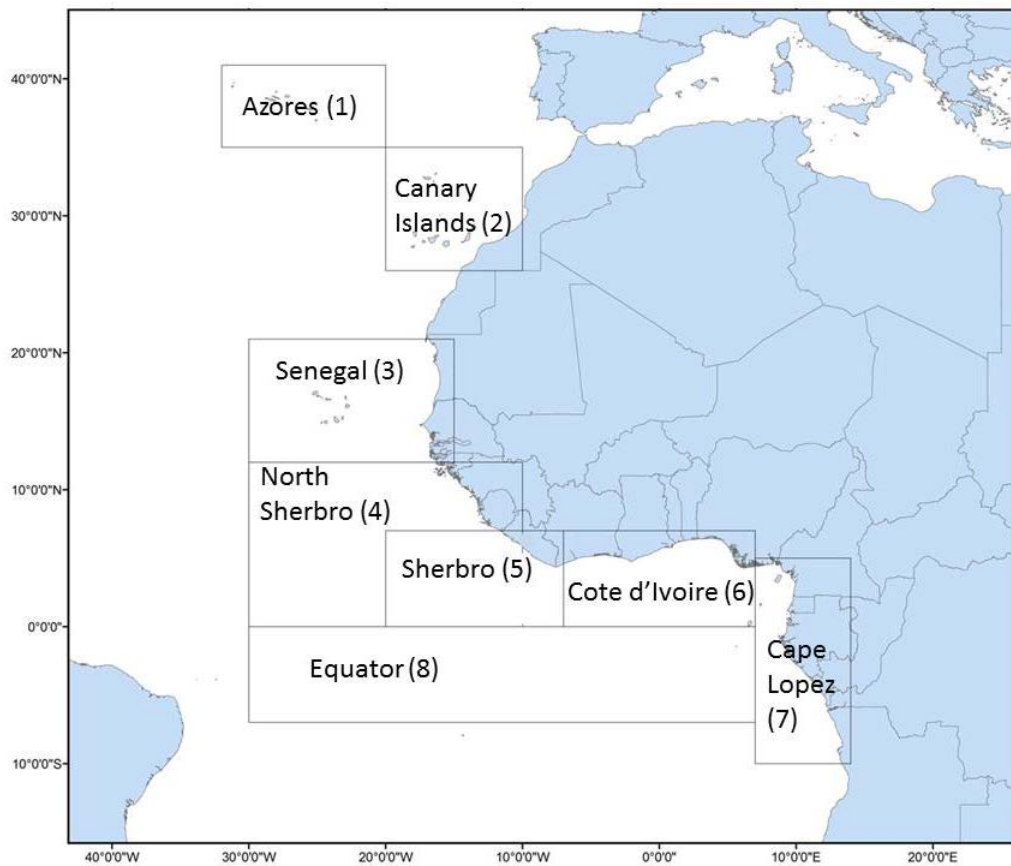
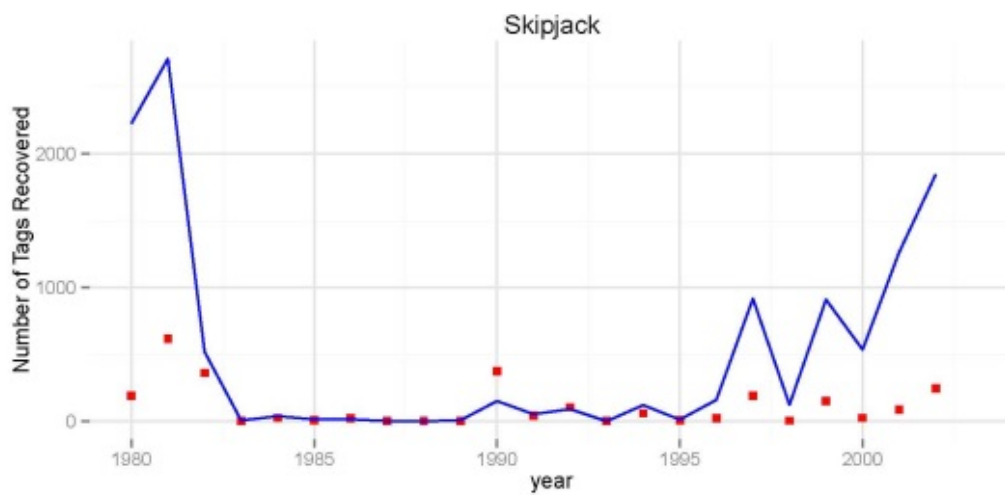
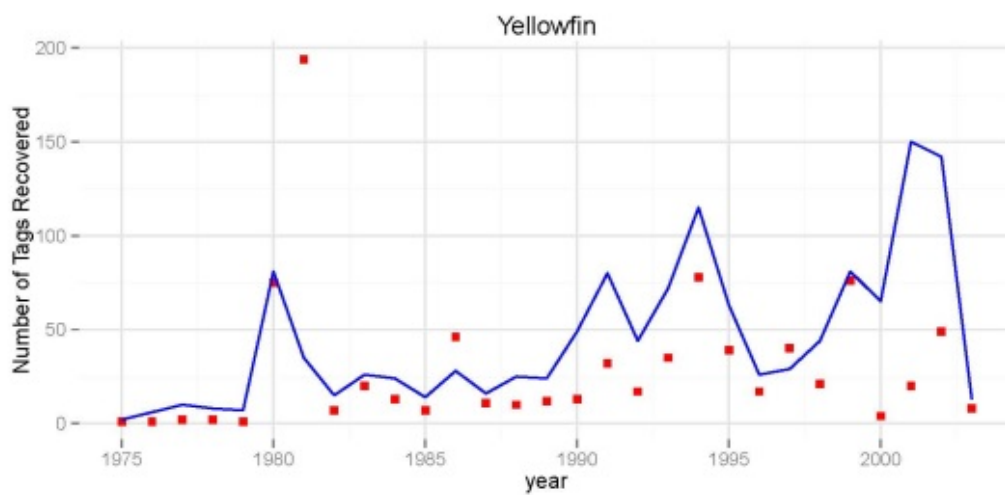
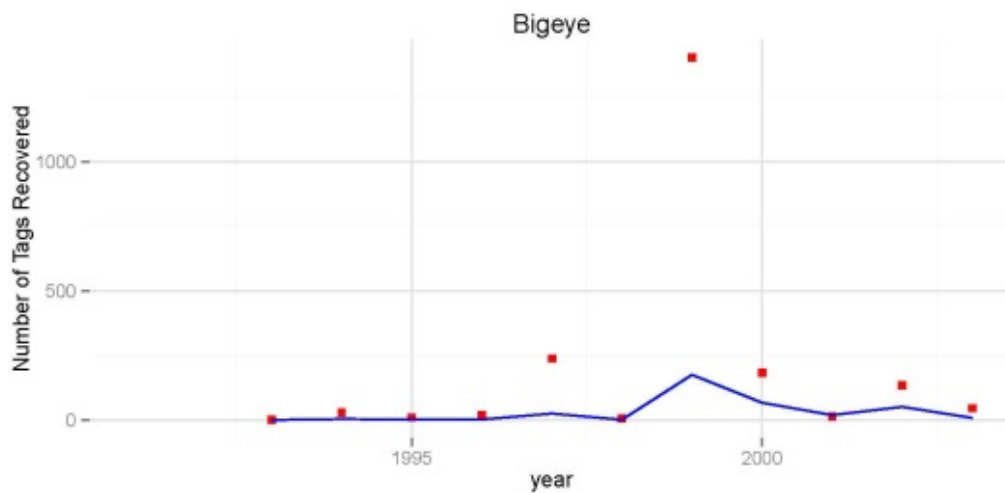


Figure 2.2 Eight region model used to standardize CPUE data for all three species.

Figure 2.3. Annual number of bigeye (top), yellowfin (center), and skipjack (bottom) tuna tag recoveries estimated by the model (blue line) and observed (red dots).



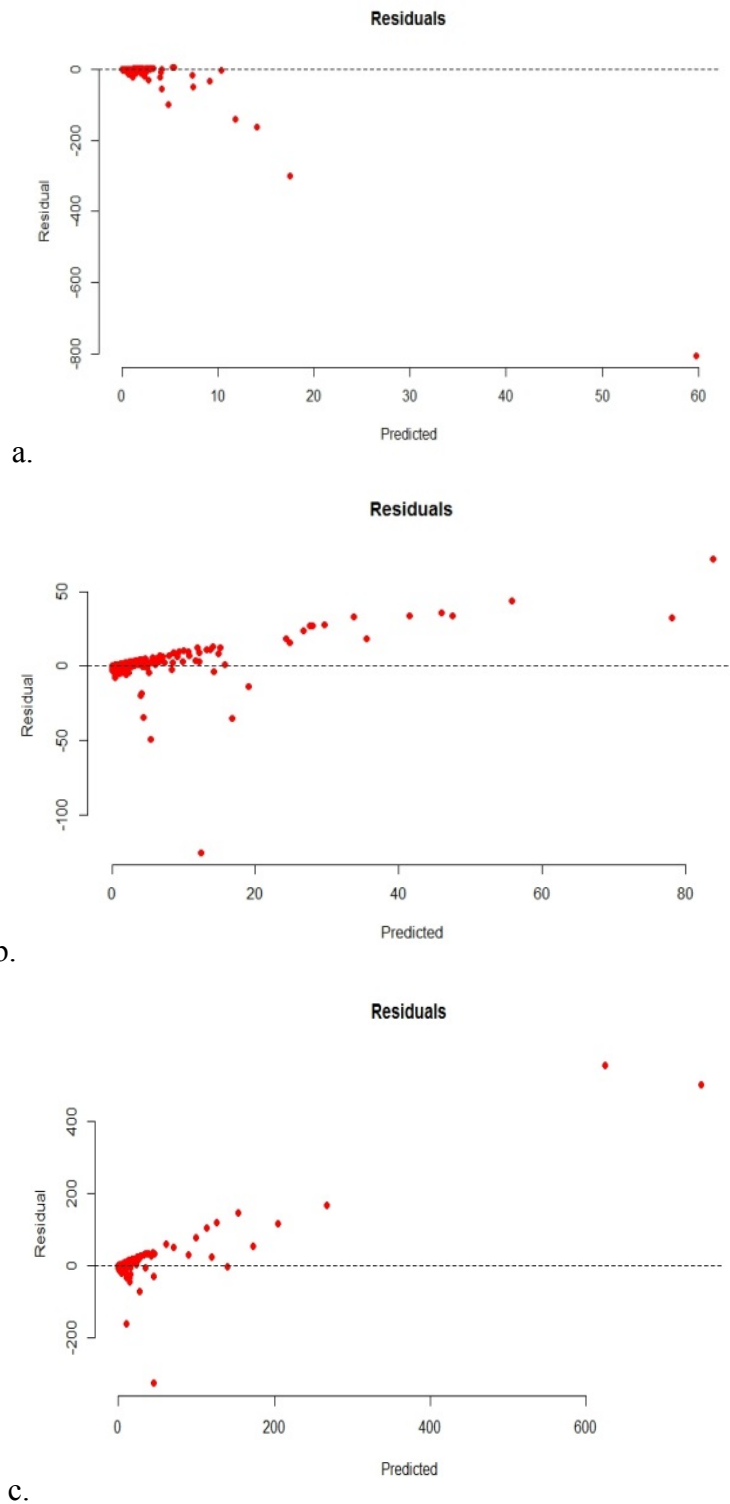
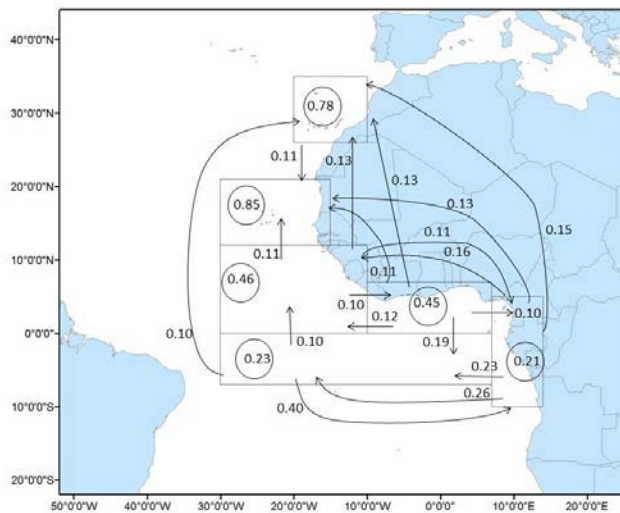
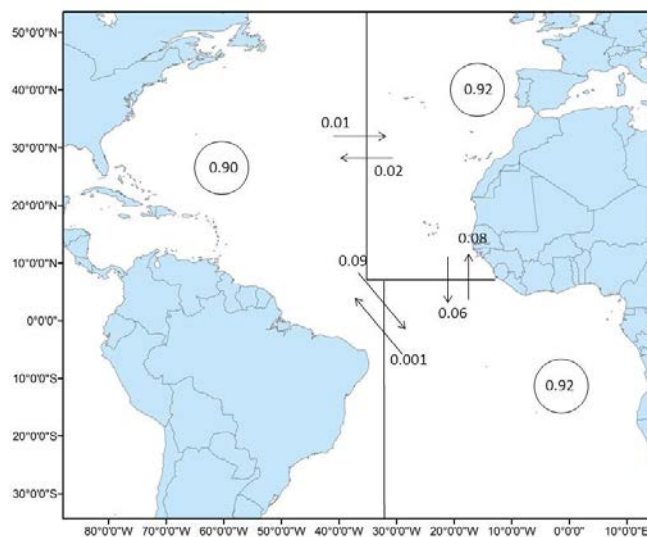


Figure 2.4. Plot of residuals of tag returns from a.) bigeye, b.) yellowfin, and c.) skipjack tuna models.

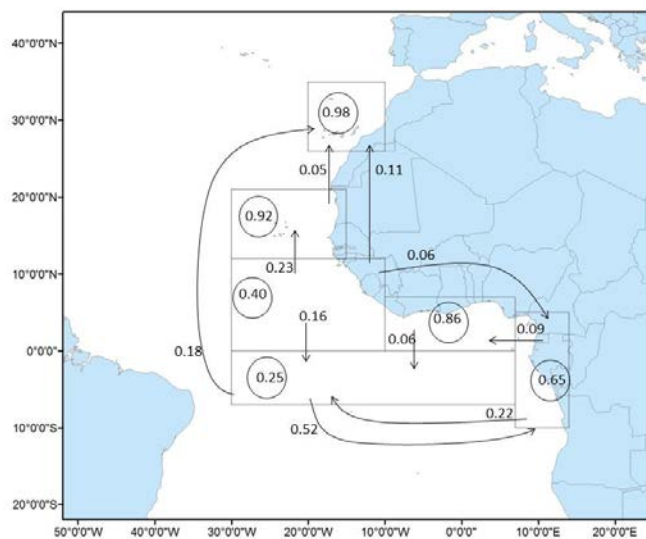
Figure 2.5. Map of estimated movement rates greater than 0.10 (arrows) and residency rates (circles) for each of the eight regions for the bigeye (top), yellowfin (center), and skipjack (bottom) tuna tagging data. Table of movement rates and CV between each region are available in the supporting information.



a.



b.



c.

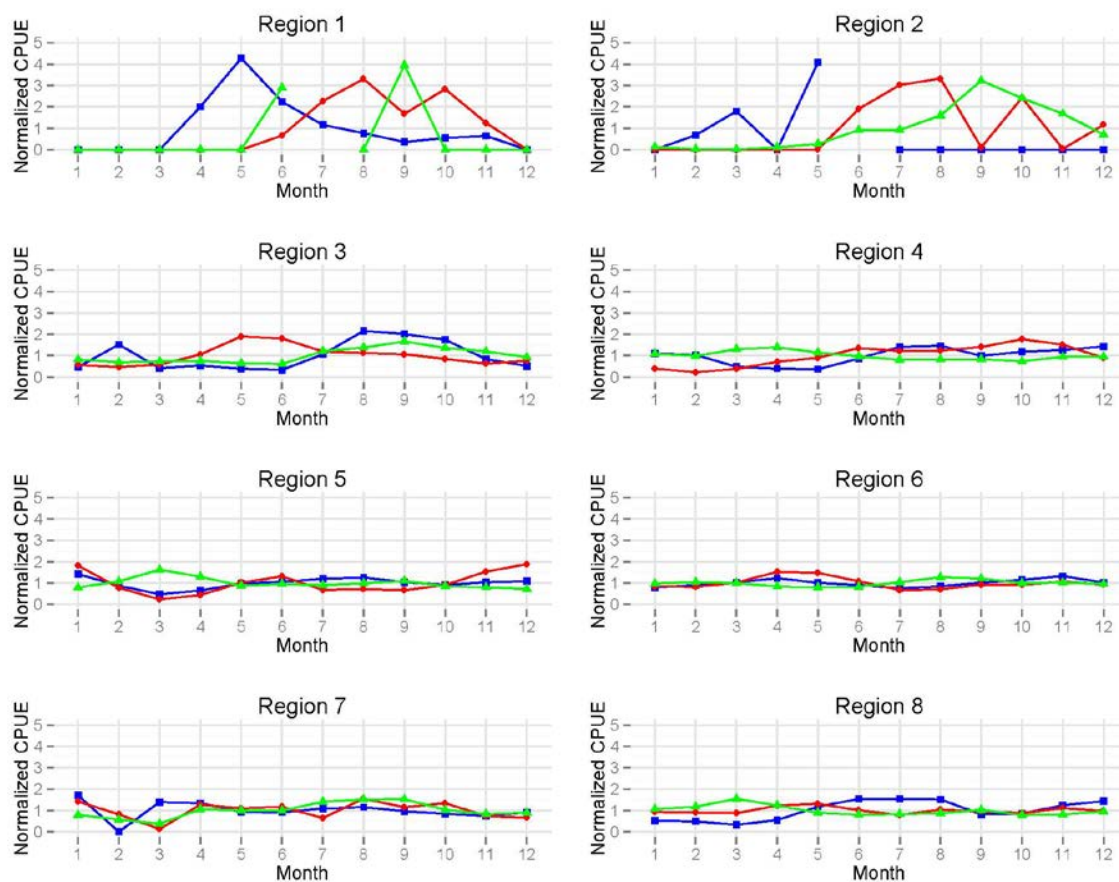


Figure 2.6. Normalized mean monthly CPUE values for each region specified in Figure 2.2 by species. Blue squares = Bigeye tuna CPUE; Red circles = Skipjack tuna CPUE; Green triangles = Yellowfin tuna CPUE.



Figure 2.7. Relative change of CPUE during the year. Colors indicate relative change in CPUE, darkest colors indicate highest CPUEs for the region, medium colors indicate large to medium CPUEs, and lightest colors indicate small but present CPUEs, white colors indicate no CPUE estimate for that month.

CHAPTER 3: A COMPARISON OF DATA STORAGE TAGS AND POP-UP SATELLITE ARCHIVAL TAGS TO BE USED IN THE ATLANTIC OCEAN TUNA TAGGING PROGRAM

Summary

Electronic tags are a valuable tool for gathering in situ data on the environment in which a tagged animal resides. They can provide a variety of parameters such as salinity, light (giving rough location estimates), temperature, depth, and acceleration. Two types of tags are often used for long term data collection on tropical tunas, internal archival data storage tags (DST) and pop up satellite archival tags (PSAT). Both types of tags have advantages and disadvantages which must be considered when designing a tagging study. The Atlantic Ocean Tuna Tagging Program (AOTTP) has a budget for electronic tagging and there has been significant debate on which type of tags should be used. A simulation was developed to mimic the AOTTP and has been used to simulate releases of both types of tags. A Bayesian space-state Cormack-Jolly-Seber model was then used to estimate movement rates from each type of electronic tagging data combined with data from conventional tags. Results show that even when DST tag returns are low, a 10% recovery rate, the data provided improves fishing and natural mortality estimates of bigeye tuna while the PSATs perform slightly better for yellowfin tuna. However, taking into account the advantages and disadvantages of each type of tag, the goals of the tagging program, and the probability that a 10% recovery rate is lower than the expected recovery rate for DSTs, the recommendation for the AOTTP is to use DSTs for their electronic tagging efforts.

Background

Tagging studies have been employed in all three major oceans of the world to provide fishery-independent estimates of many important life-history parameters in stock assessments including migration, growth rates, and natural and fishing mortality (Holland *et al.*, 2001). The majority of the tagging of the tropical tunas has taken place in the Pacific and Indian Oceans, with both regions undertaking large-scale tagging projects (Million, 2013). There have been over 800,000 tuna tagged in the Pacific Ocean and over 200,000 tuna tagged in the Indian Ocean (Leroy *et al.*, 2015). However, none of the tagging projects undertaken have included a simulation of tagging events as part of the project design. A simulation of tagging events is an important part of the project design as it provides details on what kinds of tags should be included, how tagging should be implemented, and how many tags should be released to answer the primary study questions most efficiently. These simulations have not been implemented in the past because they require insight on how to most realistically parameterize the models, which is typically only available after a large-scale project has been undertaken. Tropical tunas have a great deal of uncertainty in the essential parameters, especially migration and spawning population structure, because their migrations are much more complex than the migrations of their temperate counterparts (Leroy *et al.*, 2015).

A large-scale tuna tagging program has recently begun in the Atlantic Ocean to decrease uncertainty in many of the important stock assessment parameters (Million, 2013). The International Commission for the Conservation of Atlantic Tunas (ICCAT) Standing Committee on Research and Statistics (SRCS) has secured funding for the project, with the goal to release around 100,000 yellowfin tuna, skipjack tuna, and bigeye

tuna with conventional dart tags as well as a number of yellowfin and bigeye tuna tagged with electronic tags. A successful tagging program will allow for improved estimates of stock assessment parameters which, in turn, will allow for more accurate evaluations of the stock status for each of the three tropical tunas. The success of any tagging program is dependent upon having an appropriate tagging design in order to meet the goals of the program, implementing the tagging design successfully, and ensuring cooperation with the fishing industry to accurately report the recovery of tags (Die *et al.*, 2013).

Thanks to the information gathered in prior large-scale tuna tagging projects that have been undertaken in the Pacific and Indian Ocean and smaller tagging projects in the Atlantic Ocean, the use of a tagging simulation is a viable tool to help design the Atlantic Ocean Tuna Tagging Program (AOTTP). Small scale tagging projects on tropical tunas in the Atlantic are especially informative for parameters such as reporting rates, tag shedding rates, and movement rates. All this information will be used to parameterize a simulation for the AOTTP, allowing for the development of a simulated tagging study to aid in the study design. The goals of the AOTTP are divisible into three components, scientific, management, and capacity building (Million, 2013). The scientific goals of this program include the following:

- Estimate the crucial assessment parameters for analytical models used in stock assessments, including age-specific natural and fishing mortality, exploitation rates, and age-, sex-, and area-specific estimates of gear vulnerability;
- Estimate growth parameters by age;
- Estimate movements of tropical tunas and confirm or adjust current assumptions of stock structure;
- Evaluate the impact of FAD usage on the population dynamics of tropical tunas;
- Evaluate interactions between fisheries.

While a simulation will not be able to account for all of the differences between the two types of tags (Leroy *et al.*, 2015), we intend to provide insight on the costs and benefits of different electronic tags available and how they contribute to meeting the goals of estimating movement rates and confirming the stock structure of yellowfin and bigeye tuna. This model will also evaluate various tagging scenarios on their ability to accurately estimate natural and fishing mortality, and movement rates. Previous simulation work has suggested that movement rates and natural and fishing mortality cannot be estimated from conventional tagging alone (Calliart *et al.*, 2014). Thus external estimates of movement rates are necessary and electronic tagging offers an excellent platform to estimate these rates for pelagic species. The AOTTP has proposed to use either data storage tags (DSTs, also known as internal archival tags) and/or pop-up satellite archival tags (PSATs) to obtain estimates of movement rates of yellowfin and bigeye tuna.

Data storage tags are implanted into the body cavity of a fish and have sensors that can record a variety of physiological and environmental parameters. They can store data at short intervals of time, even as frequent as every minute. DSTs often have one to three sensors, which can protrude from the body cavity, to measure pressure (for water depth), internal and water temperature, light level, salinity, earth's magnetic field, compass heading, tilt angle, or detailed activity and behavior from accelerometers (Cooke *et al.*, 2013b; Thorstad *et al.*, 2013). DSTs must be recovered by a fisherman or scientists in order for the data to be downloaded from the tag. In this way, DSTs are similar to conventional tags in that recovery of the data is subject to fishing and natural mortality and reporting rates.

Popup satellite archival tags are externally attached to the fish, usually near the base of the dorsal fin, and typically collect environmental parameters such as light, water temperature, pressure, salinity, oxygen concentration, and may contain an accelerometer to provide data on fish swimming behavior (Thorstad *et al.*, 2013). These data are then transmitted via the ARGOS satellite to scientists after a pre-programmed pop-off time. These tags, while much more expensive than DSTs, have the advantage that they do not rely on fishery returns to obtain the data. There are several disadvantages to using PSATs over DSTs. The data that is collected is generally much coarser in resolution, unless the tag is returned, and the duration of tag deployment is generally much shorter for PSAT tags compared to DSTs. Further, PSAT tags are large and can only be placed on large fish, unlike DSTs which can be used in small fish (Cooke *et al.*, 2013b; Thorstad *et al.*, 2013; Jepsen *et al.*, 2015). Also, PSAT tags are typically approximately 2.5-3 times more expensive than DSTs, so fewer tags may be released when budgets are fixed (Doug Bears, personal comm.). However, PSATs provide information on natural mortality and movements which are not dependent upon fishermen's behavior (Donaldson *et al.*, 2008).

A tagging simulation model was developed by Matt Laretta and Dan Goethel (in review); this model provides the opportunity to simulate both the conventional tagging and the electronic tagging activities proposed by the AOTTP and the expected data available at the conclusion of the program. First, the Laretta and Goethel model was used to generate simulated conventional tag returns and DST and PSAT data for Atlantic yellowfin and bigeye tuna. Then the simulated electronic tag data were used in a Bayesian space state model to estimate movement rates. Finally, the simulated

conventional tagging data were fitted in a space state modified Cormack-Jolly-Seber model to estimate fishing and natural mortalities using the movement rates estimated from the electronic tagging data as informative priors (Cormack 1964, Jolly 1965, Seber 1965). The sequential Bayesian space-state model allows for incorporating a diverse range of information sources, in this case electronic and conventional tags (Dortel *et al.*, 2012), allows for heterogeneity within the estimates of fishing and natural mortality, and provides a useful framework for analyzing tagging studies (Buckland *et al.*, 2004; Gimenez *et al.*, 2007; Patterson *et al.*, 2008; Royle, 2008).

This simulation work will evaluate the performance of DSTs and PSATs within the framework of the AOTTP and their ability to provide informative data to meet the goals of this program to provide advice to the program coordinators. Further, it will provide a quantified comparison between the two types of tags which each have advantages and disadvantages and address many of the concerns which come with each type of tag.

Methods

Simulation Framework

Recaptured PSAT and DST tagging data were simulated using an age-structured tagging simulation model developed by Matt Laretta and Daniel Goethel (in review) to provide monthly locations for each type of tag during the duration of their release. Yellowfin and bigeye tuna were tagged with 420 DSTs and 165 PSATs each. The number of tags released were calculated based upon an estimate of the price of each type of tag (€3-3,500 for PSATs and €1-1,500 for DSTs) and the AOTTP electronic tagging

budget; approximately one million euros are available for tagging in the first two years of the program (Doug Bears, personal comm.). While prices for electronics tags can vary greatly, these provide an approximation for the true cost differences between the two tags.

Simulated DSTs were released in a single release event equally distributed between the four regions (**Figure 3.1**) and were able to be recovered for up to two years, allowing for movements in every month including the first month. Movement rates were modeled using the bulk-transfer method (Taylor *et al.*, 2011), with the probability of a fish moving between regions each month equal to the discrete movement rate. Movements of individuals were independent from one another and fish movement in each year was only dependent upon the current location of the fish and does not depend upon previous movements (Eveson *et al.*, 2012). The simulation was parameterized so that every fish was recaptured and released alive each month during the two year time at liberty and did not experience mortality, which provided a full capture history with fish locations for each month. Then data were truncated using an individual based model which used a binomial random draw to determine if the fish survived and were recaptured in each month based upon the monthly fishing and natural mortality. Finally, if an individual was recaptured, a binomial random draw was used to determine if the fish were reported using the reporting rate. Once a fish was recaptured the fish could not be recaptured again and the capture history with annual locations was truncated at the month the fish was recaptured.

The median number of tag returns obtained from 30 simulations were run were used in the estimation model. The parameters used to simulate the tagging study are in

Tables 3.1 (yellowfin) and **3.2** (bigeye). Fishing and natural mortalities were from the previous stock assessments (Anonymous 2011, 2014b, and 2016c) such that the average fishing mortality is the fishing mortality for the entire stock estimated in the most recent stock assessment for each species (Anonymous 2011, 2014b, and 2016c). Two different reporting rates were used to evaluate how a lower than expected number of DST returns might impact the parameter estimates: the mean conventional tag reporting rate estimated in Chapter Two (**Table 2.1**) from previous tagging studies for the gears which operate in each region and half of that reporting rate. This resulted in reporting rates equal to 0.9, 0.8, 0.9, and 0.4 for regions one through four for the first DST model run and 0.45, 0.4, 0.45, and 0.2 for regions one through four for the second DST model run.

165 Simulated PSATs were released for each species in a single release event equally distributed between the four regions and were programmed to popup after one year, also allowing for movements in every month including the first month.

Assumptions about the independence of movements were the same as for DSTs. Once the full capture history was produced from the simulation using the same parameters as the DSTs, the data were truncated to reflect the expected performance of PSATs. Since PSATs do not require recovery for data transmission, the duration of data collection was simulated based upon the average time at large for PSAT tags provided for the 2015 ICCAT Bluefin tuna stock assessment (Lauretta *et al.*, 2015). The month in which a PSAT popped off and began broadcasting data was drawn from a lognormal distribution with a mean of 3.2 months and a standard deviation of 0.98. This distribution accounted for both early pop offs due to technological or mechanical defects in the tag and mortality

of the individual (Whitlock *et al.*, 2012). It was assumed that there is 100% data recovery from the tags whenever they were released from the fish.

Conventional tagging recapture data were simulated using the same tagging simulation model described for the DST model above using the reporting rates 0.8, 0.9, 0.8, and 0.4 for the four regions. Fishing mortality, natural mortality, and movement rates are the same as those used to simulate the electronic tags. Fish were tagged on the first day of each year for 36 months, with an additional 24 months of recoveries after the last tagging event. Fishing effort was assumed to be uniform throughout the entire year. Two hundred fifty tags were released in each region in each month, resulting in a total of 36000 tags released for each species.

Estimation Model

The DST and conventional tag recapture data were analyzed using a combined Bayesian space-state Cormack-Jolly-Seber model (Gimenez *et al.*, 2007; Royle, 2008; Eveson *et al.*, 2012). This space-state model had three components: two process models and observational models with likelihoods for the unobserved or partially observed individual survival state process and the movement between regions; and the observational model with the likelihood conditional on the state processes (Royle, 2008). By using this type of a model we can create an individual based model where the detection probabilities are dependent upon the individual's state, in this case if the fish has survived and in which region the fish is located. Explanations for all symbols (indices, data, and model parameters) used for this analysis are provided in **Table 3.3**.

A combined model was used to simultaneously estimate movement rates, natural mortality, and fishing mortality from the combination of electronic tags and conventional

tags. From the simulated data we had $N=420$ individual DST capture histories with $T=24$ monthly sampling periods and $N=36000$ individual conventional tag capture histories with $T=5$ annual sampling periods. The capture history for individual i first captured at time f_i was the vector $R_{i,t}$ for sampling periods t at f_i through T . The two state processes described the process of being alive after the first time step and the process of moving between regions. The survival state process was a vector describing if the animal is alive at time t based upon a Bernoulli process where the probability of being alive at time t was dependent upon the state (alive or dead) in time $t-1$

$$S_{i,t} = e^{-M} * A_{i,t} \quad 3.1$$

where M was the natural mortality rate and $A_{i,t}$ is the alive vector so that if an animal is dead its probability of survival is zero, and if it is alive its probability of survival was e^{-M} . Tags which were not returned were known to be alive in the first time step but were unknown (NA) afterwards. It was assumed that all returned DST tags would provide perfect data on whether the animal was alive or dead in each time period (A). For the individuals with conventional tags, animals which were recovered provided perfect data on whether the animal was alive or dead, and the unobserved individual's state was estimated using a Bernoulli likelihood. Thus, the survival parameters could be estimated by a Bernoulli likelihood equal to:

$$L(S|A) = \prod_{i=1}^N \prod_{t=1}^T S_{i,t-1}^{A_{i,t}} (1 - S_{i,t-1})^{1-A_{i,t}} \quad 3.2$$

where $A_{i,t}$ was an ixt data vector of indicators if the individual i was alive (1) or dead (0) at time step t and $S_{i,t-1}$ is the probability of surviving the previous time period.

The movement state process was a matrix describing which region the individual was in at sampling period t where the location of the fish was assumed to be known for the individuals with electronic tags during all time periods at large, but were only known at release and the time period of recovery for the individuals with conventional tags. The value of incorporating the DST data was that the calculations of the probability of a fish being in a region during a given time period was simpler than those calculations for the conventional tag data because the location of the fish in intermediate time periods was known while all possible movements for individuals with conventional tags had to be accounted for (Eveson *et al.*, 2012). Movements for individual i in sampling period t were described by a categorical process with four possible outcomes where the location in the first time period was giving by the probability $P_{k,l}$ for the movement rates for an individual i to move from the mark region k to one of other three regions l or to remain in the mark region and in subsequent time periods, the probability an individual to move from the region in the previous time period ($m_{i,t-1}$) to one of the other three regions or to remain in the same region. The true positions in each time period were entered as data for both the electronic and conventional tags, so that the movement parameters could be estimated with the following likelihood:

$$L(P_{k,l}|m_{i,t-1}, m_{i,t}) = \prod_{k=1}^4 P_k \quad 3.3$$

m is an ixt data matrix giving the location of the individual i in time period t if the fish was observed or NA if the fish is not observed.

The recapture observational model for the conventional tag and the DST tag recaptures and the DST tag recaptures was a Bernoulli process where the probability of

being detected, $C_{i,t}$, was conditional upon the individual being alive at sampling period t and in region k . If $A_{i,t}$ was 0 then the $C_{i,t}$ was 0; an animal which was dead cannot be recovered. If $A_{i,t}$ was 1, then

$$C_{i,t} = \theta_{k,i,t} * r_k \quad 3.4$$

where $\theta_{k,i,t}$ was the probability of recovering an individual i in region k in time period t and r_k was the reporting rate in region k . The probability of recovering an individual θ in each region k is a function of the instantaneous fishing mortality rate F in region k

$$\theta_k = 1 - e^{-F_k} \quad 3.5$$

The likelihood for the tag recapture data was equal to:

$$L(C_k|R) = \prod_{i=1}^N \prod_{t=1}^T C_k^{R_{i,t}} (1 - C_k)^{1-R_{i,t}} \quad 3.6$$

where C_k is the probability of being recaptured in region k and $R_{i,t}$ is an ixt data matrix indicating whether the individual i is recaptured in the time period t with 1 being recaptured and 0 otherwise.

Natural and fishing mortality rate priors for the combined DST-conventional tag model were uninformative uniform priors with bounds at 0 and 10. The prior for $P_{k,t}$ was an uninformative dirichlet prior where alpha = 1 for each region.

The combined PSAT and conventional tag model used the same model structure for the conventional tag return data as the DST and conventional tag models. However, because PSAT returns did not depend upon fishing mortality and reporting rates as the data were transmitted independently from the fishery, the probability of the data being transmitted and the monthly location had to be modeled differently. The process of a tag popping off each month and transmitting data was modeled as a Bernoulli process where

the probability of the tagging data being transmitted U in a month has an uninformative beta prior. The tag return data thus has a Bernoulli likelihood equal to:

$$L(U|R) = \prod_{i=1}^N \prod_{t=1}^T U^{R_{i,t}} (1 - U)^{1-R_{i,t}} \quad 3.7$$

where U is the probability of a tag transmitting data in the month and R is an ixt data matrix indicating whether a tag has transmitted data (1) or not (0). This popup probability includes both the monthly natural mortality, which would cause a tag to pop-off, and premature tag shedding (Musyl *et al.*, 2011; Whitlock *et al.*, 2012). Movement rates were estimated using equation 3.3, the same methods as the archival tags where the movement between regions is a categorical distribution based upon the release location in the first month or the location in the previous month for subsequent time periods. All other assumptions and prior specifications are the same as those described for the DST-conventional tag combined model.

The estimation models were run using OpenBUGS version 3.2.2 rev 1063 (Gilks *et al.*, 1994) for at least 25 000 Monte Carlo Markov Chain (MCMC) iterations with a burn in of 5 000 iterations or until convergence was reached, with a thin of 5 to reduce autocorrelation. The convergence of the MCMC to the stationary posterior distribution was evaluated by the Gelman-Rubin diagnostic, based on the ratio of inter-chain variance to intra-chain variance (Gelman & Rubin, 1992) as well as the trace plots of each estimated parameter. Results were analyzed using R 2.15.2 (R Computing Team, 2014).

Results

The total number of DSTs returned for yellowfin tuna was 72 tags with an average time at large of 13.1 months and for bigeye tuna was 86 tags with an average

time at large of 13.3 months. This represents a return rate of 17% and 20% for yellowfin and bigeye tuna, respectively. The average time at large for PSATs for both species was 3.4 months. The return rate for yellowfin tuna conventional tags was 15% with 5 469 tags returned and for bigeye tuna was 20% with 7,157 tags returned (**Table 3.4**).

Results for the yellowfin tuna models suggested that both types of electronic tags provide similar amounts of information and resulted in very similar parameter estimates for both fishing and natural mortality (**Table 3.1**). This held true even when return rates were only 10% instead of 17% (Appendix C). Fishing mortality was underestimated by the models for all four regions, although the differences between the estimated parameter and the actual parameter used to populate the simulation were all less than 0.05, a small but significant difference between the two (**Figure 3.2**). Natural mortality was overestimated with the difference between the actual parameter 0.6, and estimated parameter, 0.73, only 0.1 (**Figure 3.3**). Movement rates are generally overestimated with both types of tags, although when movement rates are >0.01 , the model produces reasonable estimates. When movement rates are small the model significantly overestimates the parameter, however because these rates are so small it is possible that a single tag return could significantly change the parameter estimate, so the magnitude of the parameter estimates should be considered when evaluating the large biases associated with the estimates.

Results from the bigeye models are similar to the yellowfin models, where parameter estimates are the same for natural mortality and fishing mortality in regions one and three (**Table 3.2**). In region two, DST tags provided a less biased estimate of fishing mortality while PSAT tags provided a better estimate of fishing mortality in

region four. Fishing mortality was underestimated for all four regions by both models, although the difference between the actual parameter and the estimated parameter are all small (**Figure 3.4**). Natural mortality was overestimated by both models, and like yellowfin tuna, the estimated was around 0.1 greater than the actual parameter (**Figure 3.5**). Additionally, movement rate parameter estimate biases are much smaller for the DST models than the PSAT models, even for very small movement rates.

Discussion

Discussions on whether data storage tags or pop up satellite archival tags are better for long term in situ data collection have taken place for almost as long as they have been available for use. Both types of electronic tags have their advantages and disadvantages, and it sometimes appears that the best tag for a study is ultimately determined based upon the scientist's preference. This research provides a quantitative comparison of how using the two types of tags to estimate movement rates to informs fishing and natural mortality parameters differently in a spatially explicit model, taking into account some of the differences between the tags. The results appear to be inconclusive. Yellowfin tuna results suggest results are so similar that either tag would likely produce satisfactory results in the AOTTP. Bigeye tuna results show that the types of tags produce contrasting results in regions two and four, the two regions with the largest movement rates. The movement rates for yellowfin tuna are much smaller than those for bigeye tuna and may explain why incorporating electronic tags impacts the regions which have the largest movement rates for bigeye tuna. It is expected that for fish that have higher movement rates (and subsequently lower residency rates) high quality, long term data on their movements would significantly improve the movement

rate estimates and subsequently the natural and fishing mortality estimates from the conventional tag model. The movement rates used in this study are based upon those estimated in Chapter two and expert advice from scientists involved in the development of the AOTTP (Caillart *et al.*, 2014). If the movement rates of these two species are larger, we would expect a much more significant influence of the type of electronic tags released on the fishing and natural mortality parameter estimates.

The DST model parameterization results in a recovery rate of approximately 20% and a mean time at liberty of just over thirteen months. Previous DST studies on both tropical tunas and bluefin tunas have resulted in much higher recovery rates and longer times at liberty. The conventional tagging model even has a similar recovery rate, and it would be reasonable to assume a similar or even higher recovery rate for archival tags because they are recovered in the same manner as conventional tags and are often given a higher reward which may result in a higher reporting rate. In previous studies on bluefin tuna, recovery rates for DSTs are 6-60% for tag returns with usable data (for many studies this means being at liberty for more than 90 days) with recovery rates between 7-29% for tags at liberty for over a year (Block *et al.*, 2005; Kitagawa *et al.*, 2007; Walli *et al.*, 2009; Boustany *et al.*, 2010; Whitlock *et al.*, 2012; Teo *et al.*, 2013; Quílez-Badia *et al.*, 2015). Mean time at liberty for these recoveries are between one year and three years, all much longer than the mean time at liberty used in this model (Walli *et al.*, 2009; Boustany *et al.*, 2010). For yellowfin and bigeye tuna, the recovery rates have been between 16-53% in the Pacific Ocean, similar to bluefin tuna, although mean time at liberty is smaller for these species, around six months

(Schaefer and Fuller, 2002; Schaefer *et al.*, 2007; Schaefer and Fuller, 2010; Schaefer *et al.*, 2014; Schaefer *et al.*, 2015), although these mean times at liberty include fish recovered less than 90 days after release, unlike those above for bluefin tuna. In several of the studies, there are many fish at large for over a year, and the maximum time at liberty for bigeye is 1500 days, or over 4 years (Schaefer and Fuller, 2010), with several other fish at liberty for two-three years. However, when the models were run assuming a 10% return rate for DST tags, estimated parameters were still similar to those estimated by the PSAT tag models (Appendix C). This suggests that even if DST tags are returned at a lower rate than conventional tags, they provide sufficient information to inform the natural and fishing mortality parameter estimates.

Compared to previous tagging efforts with PSATs, our modeled parameters appear to be in line with the expected behavior of the tags. We assumed that PSATs had a 100% recovery rate, so that regardless of when a tag pops off, the data is successfully transmitted in full to the ARGOS satellite and the scientists. However, in most cases, transmission rates are less than 100%, on bluefin tuna studies they have been between 50-90% (De Metrio *et al.*, 2003; Stokesbury *et al.*, 2004; Block *et al.*, 2005; Stokesbury *et al.*, 2007; Musyl *et al.*, 2011; Quílez-Badía *et al.*, 2015). The mean time at liberty for PSATs in this study is also within the expected range from previous literature, ranging from 85 to 209 days (De Metrio *et al.*, 2003; Stokesbury *et al.*, 2007).

While this simulation work attempts to address several of the major difference between DSTs and PSATs, it is important to remember that it cannot account for all of the advantages and disadvantages between the two. PSATs have several significant advantages over DSTs, specifically the ability to collect the data independent of tag

returns. These tags collect significant external environmental data and transmit the summaries of the data via satellite. If any tags are returned by fishermen due to their being easy to detect, more detailed data can be obtained and the tag could be reused (Thorstad *et al.*, 2013; Jepsen *et al.*, 2015). It is also much easier to tag a fish with a PSAT than a DST; taggers require much less training and it takes less time. Also, fish do not always need to be removed from the water to tag them, which reduces handling time (Cooke *et al.*, 2013b; Jepsen *et al.*, 2015). Finally, it is possible to obtain estimates of natural mortality from PSATs and obtain data from fish which have died, which is not possible for archival tags which required recoveries from the fishery (Donaldson *et al.*, 2008; Thorstad *et al.*, 2013).

However, there are significant disadvantages to using PSATs, which may be more important depending upon the goals of the tagging program. First, PSATs are relatively large and limited to being used on large individuals (Thorstad *et al.*, 2013). The simulation model did not take size or age into account when tagging fish with electronic tags, although it may be useful to include age or size structure in future work. In the AOTTP, it is expected that the majority of the fish tagged are less than 100cm due to tagging occurring on baitboats (Million, 2013). These fish are too small for tagging with PSATs; therefore it would be necessary to tag the largest adult yellowfin and bigeye selectively during the tagging process. This may even require a separate tagging procedure to target these larger fish, which would increase the costs of the program. This means that the electronic tags will not provide information on the juvenile fish which the conventional tagging program will predominately tag. Thus, assuming that the movements of juvenile tropical tuna are different than those of adult tropical tuna, the

information from the PSAT tagging cannot be combined with that from the conventional tagging data, rendering the use of the data limited for estimating stock assessment parameters. Adult and juvenile movement may differ for both yellowfin tuna and bigeye tuna. Juvenile bigeye tuna remain close to the surface and associate with fish aggregating devices (FADs) in mixed species groups while adult bigeye tuna remain close to the thermocline and make periodic excursions into the mixed layer (ICCAT, 2013). Yellowfin show less drastic behavioral changes, although adults tend to make deeper dives than juveniles, and often form free swimming schools while juvenile yellowfin tuna are usually found in mixed species schools around FADs.

Another disadvantage to using PSATs is the possibility that the large tag may impact swimming behavior. Because PSATs are often large and are external, fish may experience increased drag due to the positive buoyancy of the tag, which can be increased via biofouling (Thorstad *et al.*, 2013). This can increase the energy expenditure of the fish and/or injure the swimming muscles of the fish which can significantly reduce swimming performance. This could disrupt, delay, or reduce migration for migrating species (Thorstad *et al.*, 2013; Jepsen *et al.*, 2015). For the AOTTP, one of the uses of electronic tagging is to estimate movement rates since both yellowfin and bigeye tuna are highly migratory species. Using an electronic tag which may significantly change an individual's behaviors such that the movements of that individual are decreased, changed, or eliminated would mean that the data collected from those tags are not representative of the whole population and erroneous conclusions about the stock structure and fish movements may be drawn.

PSATs are known to provide incomplete datasets, which can limit the usefulness of the data collected. This can be either due to problems with transmitting the data to a satellite or early detachment of the tag. While PSATs are not dependent upon fishermen to return the data, there can be many occurrences which cause significant holes in the data transmission. Data transmission could be disrupted due to weather, surrounding topography, and short battery life of the tags (Cooke *et al.*, 2013b; Thorstad *et al.*, 2013).

Early tag pop-offs are addressed in the simulation for the PSATs and this is an important factor to take into account when deciding to use PSATs in a tagging study. Due to a variety of reasons, including battery failure, mechanical failure, mortality, biofouling, infection and tissue necrosis, expansion and contraction of the electronics, batteries, and pressure housing due to rapid vertical movements, shark predation, and human error, the majority of PSATs last between 10s and a few hundreds of days (Musyl *et al.*, 2011; Jepsen *et al.*, 2015). Previous studies have reported that 54% of tags pop off 6-9 months before its preprogrammed date (Teo *et al.*, 2013) and it is estimated that 82% of all PSATs attached pop off early (Musyl *et al.*, 2011). Many of the occurrence that may cause premature pop-offs are a concern for bigeye and yellowfin tuna, specifically the problems due to rapid diving behavior, which is common for both species (Schaefer *et al.*, 2009; Schaefer and Fuller, 2010).

Other disadvantages of using PSATs for the AOTTP include the possibility that the tag may grow out of a fast growing fish, which would be a problem when tagging young yellowfin and bigeye tuna (Thorstad *et al.*, 2013; Jepsen *et al.*, 2015). Also, PSAT tags are very expensive while the AOTTP only has a limited budget for electronic tagging (Cooke *et al.*, 2013b). The simulation suggests that reasonable results can be obtained

using the entire AOTTP budget for PSATs, although the risk of significant tag loss which is not addressed in this study may decrease the usefulness of the PSAT data.

Data storage tags have several advantages over the use of PSATs for the AOTTP. DSTs have the capability to store higher resolution, continuous data than PSATs and can collect physiological data on the individual fish in addition to the environmental data (Ådlandsvik *et al.*, 2007; Cooke *et al.*, 2013b). These tags are also much smaller than PSATs and can be put into much smaller fish (Thorstad *et al.*, 2013). This would allow the AOTTP to tag the small juvenile fish in addition to the large adult yellowfin and bigeye tuna providing data on all life stages of the fish. This would allow for comparisons between the behaviors of the fish at each life stage and for the integration of the electronic data with the conventional tag data to provide robust estimates of important population parameters such as natural and fishing mortality.

Furthermore, DSTs do not impact the streamlined body shape of the fish, which means that unlike PSATs, they will not significantly impact swimming behavior (Thorstad *et al.*, 2013). While there can be short term impacts of the surgical implantation of the tags, including inflammation and behavioral changes, the long term effects are minimal once the incision heals (Jepsen *et al.*, 2002). This means that data collected from the recovered tags are likely to represent the entire population of fish. A disadvantage of using DSTs is that significant training is necessary to implant tags into the individual fish (Thorstad *et al.*, 2013; Jepsen *et al.*, 2015); however for the AOTTP, dedicated tagging teams are being used to tag fish, so these impacts will be minimal.

The major disadvantage to using DSTs is that data retrieval is dependent upon the tag being recaptured and reported by fishermen (Cooke *et al.*, 2013b). This means that

many more tags are required to be released in order to obtain high enough tag returns that data is informative. Since previous studies have shown recovery rates higher than those used in the simulation, and the recovery rates of conventional tags in this simulation are over twice those used for the DSTs, we would expect that the use of DSTs in the AOTTP would provide informative data even with a lower than expected recovery rate. Also, because the returns within a region are dependent upon fishery returns, it is possible that the tags which are recovered are from fish who are residents or who return to the area every year and fish which move outside of the fishery may be missed. This would give an incomplete picture of the actual movements of the fish. However, because the fisheries for both yellowfin and bigeye tuna cover a large portion of the Atlantic, this may not be a significant problem. Inconsistent reporting rates in different regions may also impact the interpretation of DST data as more tags will be recovered from areas which have higher visibility of the recovery program. Since the AOTTP is an Atlantic-wide endeavor, it is hoped that significant tag recovery efforts will occur in all regions (Million, 2013) which would reduce the impact of this problem and the alternative models run with 10% return rate for DST tags suggest that a reduced return rate will not impact the fishing and natural mortality parameters estimated from the conventional tag data.

Making the decision between DSTs and PSATs for a tagging study requires an in depth analysis and comparison between the two types of tags. Many things must be taken into account when doing these comparisons, the size and species of the fish being tagged, the goals and expected outcomes of the tagging study, and the budgetary restrictions. The results of the simulation are within the expected range of recovery rates and amount

of information gathered for both tags. Taking into account the goals of the AOTTP, which includes long term data collection for the estimation of movement rates and confirmation of stock structure, the simulation results and the discussion of the advantages and disadvantages of the two different tags support the conclusion that either the DSTs or the PSATs would provide adequate information on movements to inform the conventional tag model. Whether it is best to release only one of the types of electronic tags or to release some of each is a discussion that would require taking into account the other goals of the AOTTP. However, this would require releasing fewer of each types of electronic tag, and reduced numbers of tags released was not evaluated by this research. It is vital to perform these kinds of analyses in order to maximize the success of an electronic tagging study.

Table 3.1. Parameters used to populate the tagging model (Actual) and estimates, percent biases, and CVs for each of the electronic tagging models for yellowfin tuna.

	PSAT Model				DST Model		
	Actual	Estimate	Percent Bias	CV	Estimate	Percent Bias	CV
F Region 1	0.18	0.13	-27%	0.03	0.13	-27%	0.03
F Region 2	0.21	0.16	-25%	0.05	0.16	-25%	0.05
F Region 3	0.18	0.14	-24%	0.04	0.13	-25%	0.04
F Region 4	0.08	0.06	-26%	0.07	0.06	-25%	0.07
M	0.6	0.73	22%	0.02	0.73	22%	0.02
P[1,1]	0.948	0.95	0%	0.00	0.95	0%	0.00
P[1,2]	0.05	0.04	-14%	0.10	0.05	-7%	0.09
P[1,3]	0.001	0.002	123%	0.44	0.002	126%	0.40
P[1,4]	0.001	0.002	150%	0.66	0.006	498%	0.53
P[2,1]	0.05	0.03	-36%	0.11	0.04	-28%	0.10
P[2,2]	0.6	0.68	13%	0.03	0.68	14%	0.03
P[2,3]	0.15	0.12	-20%	0.07	0.12	-19%	0.07
P[2,4]	0.2	0.17	-15%	0.10	0.16	-20%	0.09
P[3,1]	0.001	0.002	58%	0.49	0.002	64%	0.38
P[3,2]	0.15	0.13	-16%	0.07	0.13	-17%	0.07
P[3,3]	0.799	0.82	3%	0.01	0.84	5%	0.01
P[3,4]	0.05	0.05	-2%	0.17	0.04	-24%	0.17
P[4,1]	0.001	0.001	-23%	0.73	0.001	16%	0.50
P[4,2]	0.2	0.19	-7%	0.06	0.18	-9%	0.06
P[4,3]	0.05	0.04	-24%	0.12	0.03	-32%	0.12
P[4,4]	0.749	0.78	3%	0.02	0.78	4%	0.02

Table 3.2. Parameters used to populate the tagging model (Actual) and estimates, percent biases, and CVs for each of the electronic tagging models for bigeye tuna.

	PSAT Model				DST Model		
	Actual	Estimate	Percent Bias	CV	Estimate	Percent Bias	CV
F Region 1	0.24	0.20	-17%	0.03	0.20	-19%	0.03
F Region 2	0.24	0.20	-17%	0.04	0.24	-1%	0.03
F Region 3	0.12	0.10	-20%	0.04	0.10	-19%	0.04
F Region 4	0.12	0.11	-9%	0.05	0.05	-57%	0.05
M	0.4	0.54	34%	0.02	0.53	32%	0.02
P[1,1]	0.749	0.81	9%	0.01	0.80	7%	0.01
P[1,2]	0.2	0.16	-22%	0.05	0.16	-20%	0.04
P[1,3]	0.001	0.001	41%	0.57	0.003	196%	0.38
P[1,4]	0.05	0.03	-44%	0.16	0.04	-28%	0.13
P[2,1]	0.2	0.15	-27%	0.05	0.16	-18%	0.05
P[2,2]	0.65	0.75	15%	0.02	0.72	10%	0.02
P[2,3]	0.05	0.04	-26%	0.12	0.04	-19%	0.12
P[2,4]	0.1	0.07	-29%	0.11	0.08	-21%	0.11
P[3,1]	0.001	0.001	8%	0.50	0.002	108%	0.36
P[3,2]	0.05	0.03	-45%	0.10	0.03	-45%	0.10
P[3,3]	0.749	0.84	13%	0.01	0.82	10%	0.01
P[3,4]	0.2	0.13	-36%	0.08	0.15	-27%	0.08
P[4,1]	0.05	0.03	-38%	0.10	0.04	-28%	0.09
P[4,2]	0.1	0.07	-27%	0.07	0.07	-27%	0.07
P[4,3]	0.2	0.16	-22%	0.07	0.17	-16%	0.07
P[4,4]	0.65	0.74	14%	0.02	0.72	11%	0.02

Table 3.3. List of indices, model variables, data, and model parameters used for this analysis.

Symbol	Description
Indices	
N	Number of tags released
T	Number of time periods
i	Individual
t	time period
f	Cohort
k,l	Regions
Data	
A_{i,t}	Indicator if the individual I is alive (1) or dead (0), unobserved (NA) in time period t
R_{i,t}	Indicator if the individual i is returned (1) or not (0) in time period t
m_{i,t}	Location of individual I in time period t, 1-4 if observed, NA if not
Model Parameters	
S_{i,t}	Probability of survival for individual I in time period t
C_{i,t}	Probability of detection for individual I in time period t
θ_{i,t}	Probability of recapture
M	Instantaneous fishing mortality
F_k	Instantaneous fishing mortality in region k
r_k	Reporting Rate in region k
P_{k,l}	Movement rate from region k to region l
U	Probability for PSAT tag to popup and transmit data

Table 3.4. Number of recovered conventional tags for each year, region, and species.

YFT		Region			
Year Recovered	1	2	3	4	Total
1	183	217	187	36	623
2	379	548	358	80	1365
3	447	618	485	125	1675
4	368	465	311	78	1222
5	153	220	174	37	584
Total	1530	2068	1515	356	5469

BET		Region			
Year Recovered	1	2	3	4	Total
1	263	277	122	62	724
2	575	644	307	145	1671
3	739	813	379	204	2135
4	577	621	309	166	1673
5	291	364	205	94	954
Total	2445	2719	1322	671	7157

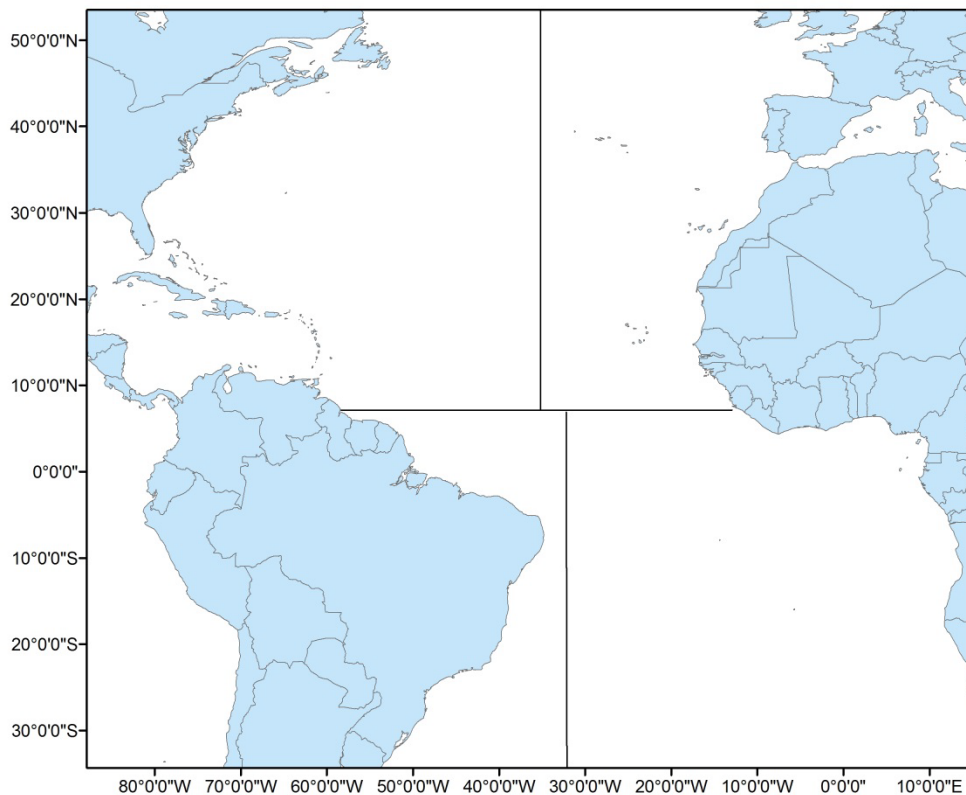


Figure 3.1. Four region model used with region one the northeast Atlantic, region two the southeast Atlantic, region three the southwest Atlantic, and region four the northwest Atlantic.

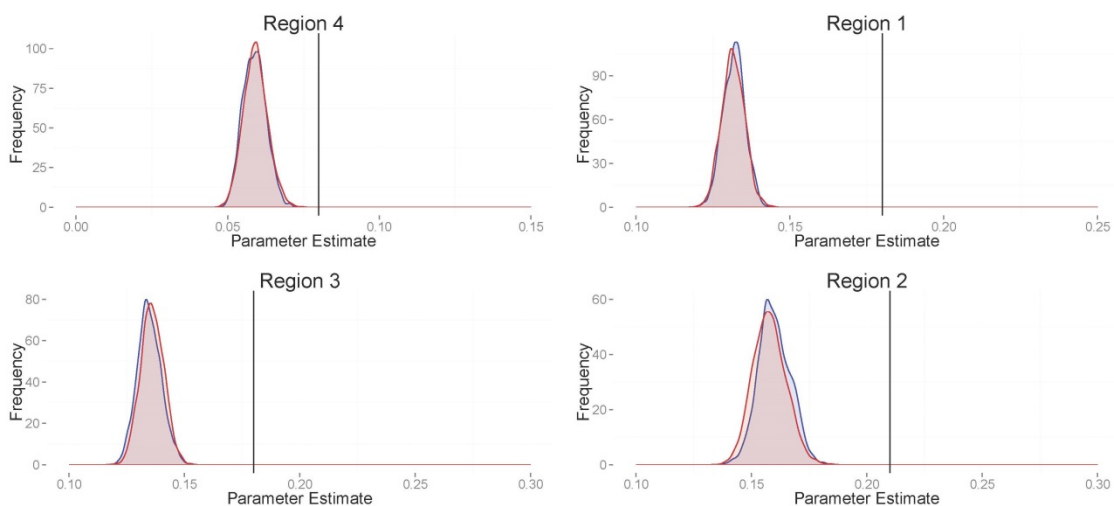


Figure 3.2. Yellowfin tuna fishing mortality posterior probabilities from the model using conventional tags combined with each of the electronic tags to estimate movement rate. Blue represents the DST model, red represents the PSAT model and the black line indicates the actual value used to populate the simulation.

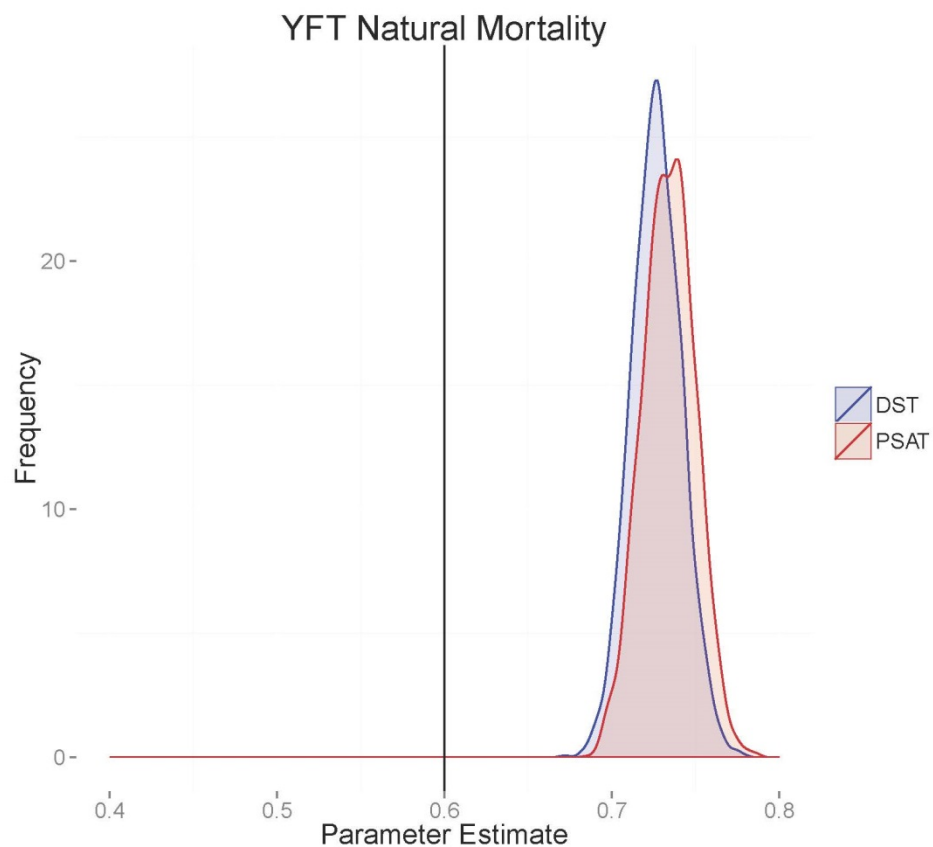


Figure 3.3. Yellowfin tuna natural mortality posterior probabilities from the conventional tag model using each of the electronic tags to estimate movement rate. Blue represents the DST model, red represents the PSAT model and the black line indicates the actual value used to populate the simulation.

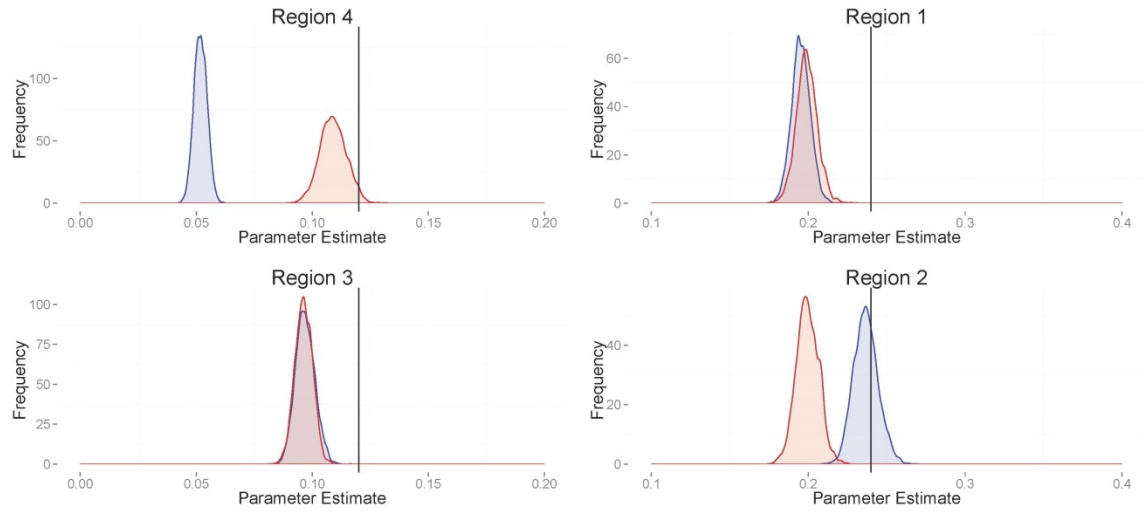


Figure 3.4. Bigeye tuna fishing mortality posterior probabilities from the conventional tag model using each of the electronic tags to estimate movement rate. Blue represents the DST model, red represents the PSAT model and the black line indicates the actual value used to populate the simulation.

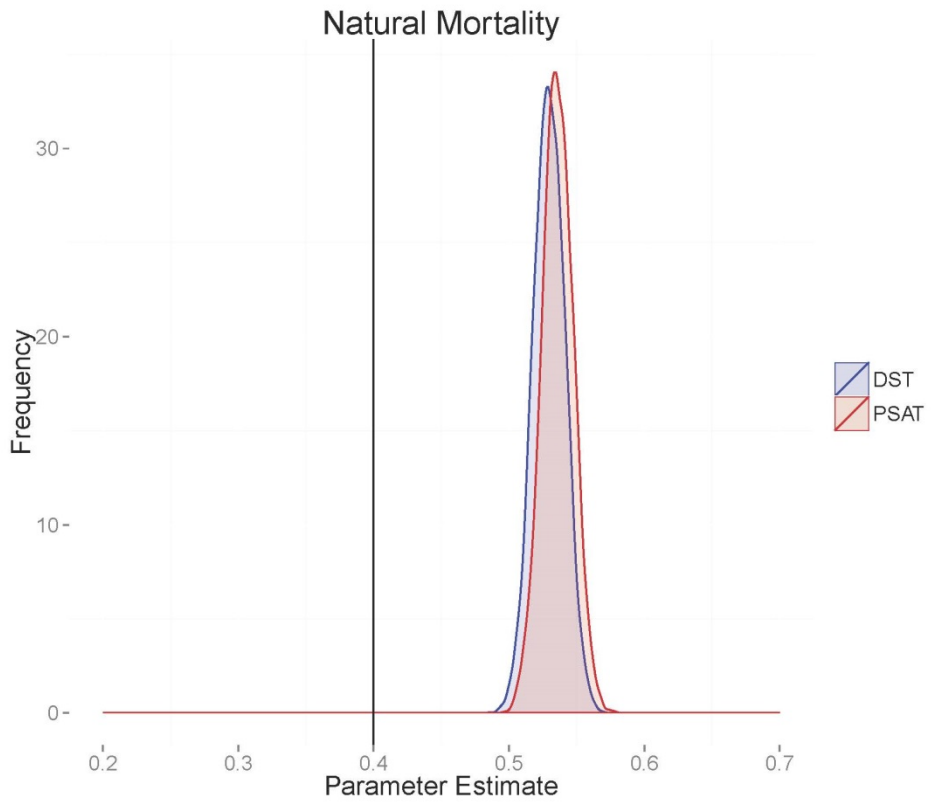


Figure 3.5. Bigeye tuna natural mortality posterior probabilities from the conventional tag model using each of the electronic tags to estimate movement rate. Blue represents the DST model, red represents the PSAT model and the black line indicates the actual value used to populate the simulation.

CHAPTER 4: ESTIMATING AGE-SPECIFIC FISHING AND NATURAL MORTALITY PARAMETERS FROM A MODIFIED CORMACK-JOLLY-SEBER SPACE STATE TAGGING MODEL FOR ATLANTIC TROPICAL TUNAS

Summary

A Bayesian space-state Cormack-Jolly-Seber model was used to estimate population parameters from simulated tagging data for Atlantic yellowfin, bigeye, and skipjack tuna. The model estimated age-specific natural mortality and age- and region-specific fishing mortality. The accuracy of these estimates was compared to the accuracy of estimates from a not age-specific model estimating a single natural mortality and a region-specific fishing mortality. Uninformative lognormal priors were used for natural and fishing mortality rates while movement rates were assumed to be known from an external source and are not estimated within the model. Yellowfin tuna results indicated that the age-specific fishing mortality parameter estimates were less biased than the not age-specific fishing mortality estimates. Yellowfin natural mortality parameter estimates are less biased when estimated using age-specific parameters from a Lorenzen curve rather than the not age-specific model. For bigeye, estimating age-specific parameters did not improve the accuracy of the parameter estimates over not age-specific estimates for natural mortality. The natural mortality estimated from the Lorenzen curve produced an appreciably positively biased parameter. However, fishing mortality estimates were improved when the parameters were age-specific. Skipjack tuna fishing mortality estimates were improved by estimating age-specific parameters, although the age specific fishing mortality parameters were highly variable in the accuracy of the parameter estimates with biases between -100% to 100% while the not age-specific model produced fishing mortality estimates had biases between -100% and 300%. Future stock

assessments should consider incorporating age-specific parameters as information becomes more available and should evaluate them on a species by species basis, as they could significantly change the conclusions on stock status.

Background

Stock assessments have historically been run assuming there was no age-specific heterogeneity in natural mortality parameters for a stock. With the development of more complex stock assessment models such as Stock Synthesis 3 and the processing power to run them, there have been attempts to incorporate age-specific natural mortality rates. Age specific fishing mortality rates are also estimated in catch-at-age models. It has long been understood that natural mortality changes over the course of a fish's life, generally decreasing with age (Brodziak *et al.*, 2011). Similarly, many fisheries have size limits or target a specific portion due to gear selectivity of a population which causes different fishing mortalities upon different ages of fish. Within tagging studies, survival and detection parameters are often estimated as constants across time or vary by year, but are rarely age-specific. The assumption in these tagging programs is that all ages are equally susceptible to tagging and recovery. In fisheries which have significant age or size selectivity, this is not a valid assumption.

The tagging program in the Atlantic tropical tuna fisheries has significant size selectivity in both the tagging process and the recapture process. The majority of yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and bigeye (*T. obesus*) tuna are tagged on baitboats, which target small sized tuna. The tuna tagged are typically between 30 and 60 cm fork length (FL), although larger tuna can be tagged from the US

rod and reel fishery in the northwestern Atlantic and the Azores baitboat fishery (Million, 2013). Recovered tuna vary in size based upon the fishery from which they are recovered. The surface fisheries typically catch smaller tuna while the longline fishery typically catches large tuna. The baitboat fishery primarily catches small tuna (30-60cm FL) around fish aggregating devices (FADs, Anonymous, 2013). These include juvenile yellowfin and bigeye as well as small skipjack tuna. The purse seine fishery catches similar sized tuna around FADs as baitboats, but also catches large adult yellowfin tuna in free schools. The longline fishery catches primarily large adult yellowfin and bigeye tuna with occasional skipjack as bycatch (Anonymous, 2013).

The differences in abundance and the size selectivity between gears result in fishing mortality rates varying with size or age. Therefore in order to accurately estimate parameters from a tagging study, this size/age structure should be taken into account in addition to the age-specific natural mortality rates already beginning to be incorporated into stock assessments. The Atlantic Ocean Tuna Tagging Program (AOTTP) offers a good opportunity to evaluate the interaction between the three fisheries as well as provide estimates of the age-specific natural and fishing mortality rates for each species (Million, 2013). To evaluate the usefulness of the tagging program, a spatially-explicit age structured tagging simulation model was developed by Matt Laretta and Dan Goethel (in review). Using simulated data from the operating model, a space state modified Cormack-Jolly-Seber model was used to estimate fishing (as the probability of capture transformed to an instantaneous rate) and natural mortalities (as the apparent survival transformed to an instantaneous rate, assuming migration rates are known) from hypothetical populations of Atlantic yellowfin, skipjack, and bigeye tuna

(Cormack, 1964; Jolly, 1965; Seber, 1965). The space-state model allows for heterogeneity within the estimates of these parameters, and provides a useful framework for analyzing tagging studies (Buckland *et al.*, 2004; Gimenez *et al.*, 2007; Patterson *et al.*, 2008; Royle, 2008).

This simulation work provides an example of how incorporating age-specific parameters may be useful to other tuna species stock assessments and tagging models by examining a suite of species which experience a range of selectivity-at-age patterns. There is very little overlap in the bigeye tuna selectivity-at-age between surface fisheries, which target exclusively juveniles, and longline fisheries, which target exclusively adults. There is much greater overlap in selectivity-at-age for yellowfin tuna between the surface and longline fisheries, as a result of the fact that purse seiners catch large adults in free schools in addition to the smaller juveniles caught on FADs and longliners catch adult yellowfin tuna as well. Skipjack tuna selectivity-at-age is fairly constant as it is targeted at all ages in the surface fisheries and not targeted in the longline fisheries. This paper simulation-tests a spatially-explicit tagging model to estimate age-specific fishing and natural mortality parameters that can be used to 1.) evaluate the improvement in parameter estimates from an age-structured model compared to a model where mortality is assumed constant across all ages, 2.) provide tagging study design advice for the upcoming AOTTP, and 3.) describe a framework to analyze the subsequent tagging data collected from the AOTTP.

Methods

Simulation Framework

Recapture data were simulated using a spatially-explicit age-structured tagging simulation model developed by Matt Lauretta and Daniel Goethel (in review) with four regions divided east and west by 32°W and north and south by 7°N (**Figure 4.1**). The parameters used to simulate the tagging study are in **Table 4.1**. Explanations for all symbols (indices, data, and model parameters) used for this analysis are provided in **Table 4.2**. Fishing mortalities were developed by assigning fishing mortalities by the relative proportion at age, based upon the catch-at-age caught in each region from the previous stock assessments (Anonymous 2011, 2014b, and 2016c) so that ages with higher catches had higher fishing mortalities and the average fishing mortality in each region is the fishing mortality for the entire stock estimated in the most recent stock assessment for each species (Anonymous 2011, 2014b, and 2016c). Natural mortalities were specified using a Lorenzen (2005) scaled natural mortality assuming a reference natural mortality for each species of 0.5, 0.17, and 0.4 for yellowfin, bigeye, and skipjack tunas, respectively. Natural mortality at age was specified such that M_a would equal M_r at age t_{\max} :

$$M_a = M_r \left(\frac{L_r}{L_a} \right) \quad 4.1$$

where L_r is the length at the reference age r and L_a is the length of the fish at age a .

Length at age was calculated using the growth curve for each species: for bigeye tuna, the Hallier *et al.* (2005) growth curve (Anonymous 2015); for yellowfin tuna, the Draganik & Pelczarski (1984) growth curve (Walter, *et al.* 2016); for skipjack, the Hallier and

Gaertner (2006) growth curve (Anonymous 2014). In addition, the simulation specifications used for creating these data are as following:

- assumed 100% reporting rates and no tag loss nor tagging mortality
- The model is spatially structured with four regions, divided by 35°W and 10°N. Region one is the northeast Atlantic, region two is the southeast Atlantic, region three is the southwest Atlantic, and region four is the northwest Atlantic.
- Movement is constant across all ages and fish can move once per year starting in the year in which they were tagged
- Six age classes were used for skipjack and yellowfin, with age five as the plus group and eight age classes were used for bigeye with age seven as the plus group
- Fish were tagged on the first day of each year for three years, with an additional two years of recoveries after the last tagging event.
- Fishing effort is assumed to be uniform throughout the entire year.
- 3000 tags are released in each region in each year, resulting in a total of 36000 tags released for each species.
- Age class is assumed to be known for all fish released.
- The median number of tag returns obtained from 30 simulations were run were used in the estimation model.

Estimation Model

The recapture data were then analyzed using a Bayesian space-state Cormack-Jolly-Seber model where the survival and detection probabilities contain individual heterogeneity (Gimenez *et al.*, 2007; Royle, 2008). The individual heterogeneity in this case is the age of the fish, although additional factors could be included as appropriate. This space-state model had three components: two process models and observational models with likelihoods for the unobserved or partially observed individual survival state process and the movement between regions; and the observational model with the likelihood conditional on the state processes (Royle, 2008). By using this type of a model we can create an individual based model where the survival and detection probabilities are age-specific and the detection probabilities are dependent upon the individual's state, in this case if the fish has survived and in which region the fish is

located. Both natural mortality and fishing mortality have the same structural form in the estimation model as in the simulation framework. This ensures that the model could estimate unbiased age-specific parameters if the data are informative. The only change between the operational and estimation models was when fishing and natural mortality were assumed to be constant across ages.

From the simulation model we have $N=36\ 000$ individual capture histories with $T=5$ sampling periods. The capture history for individual i first captured at time f_i was the vector $R_{i,t}$ for sampling periods t at f_i through T . The two state processes described the process of being alive after the first time step and the process of moving between regions. The survival state process was a vector describing if the animal is alive at time t based upon a Bernoulli process where the probability of being alive at time t was dependent upon the state (alive or dead) in time $t-1$

$$S_{i,t} = e^{-M_a} * A_{i,t} \quad 4.2$$

where M_a was the natural mortality rate at age a calculated from size at age and Lorenzen scaling of the estimated reference mortality from equation 4.1 and $A_{i,t}$ is the alive vector so that if an animal is dead its probability of survival is zero, and if it is alive its probability of survival was e^{-M} . Animals which were recovered provided perfect data on whether the animal was alive or dead, and the unobserved individual's state was estimated using a Bernoulli likelihood. Thus, the survival parameters could be estimated by a Bernoulli likelihood equal to:

$$L(S|A, a) = \prod_{i=1}^N \prod_{t=1}^T S_{i,t-1}^{A_{i,t}} (1 - S_{i,t-1})^{1-A_{i,t}} \quad 4.3$$

where $A_{i,t}$ was an ixt data vector of indicators if the individual i was alive (1) or dead (0) at time step t and $S_{i,t-1}$ is the probability of surviving the previous time period.

The movement state process was a matrix describing which region the individual was in at sampling period t where the location of the fish was assumed to be known at release and the time period of recovery. It was modeled such that fish can move to another region within the first year and can move between regions once per year. Movements for individual i in sampling period t were described by a categorical process with four possible outcomes where the location in the first time period was giving by the probability $P_{k,l}$ for the movement rates for an individual i to move from the mark region k to one of other three regions l or to remain in the mark region and in subsequent time periods, the probability an individual to move from the region in the previous time period ($m_{i,t-1}$) to one of the other three regions or to remain in the same region. The true positions in the recapture and recovery time periods were entered as data, so that the movement parameters could be estimated with the following likelihood:

$$L(P_{k,l}|m_{i,t-1}, m_{i,t}) = \prod_{k=1}^4 P_k \quad 4.4$$

where m is an ixt data matrix giving the location of the individual i in time period t if the fish was observed or NA if the fish is not observed.

The recapture observational model for the conventional tag and the DST tag recaptures and the DST tag recaptures was a Bernoulli process where the probability of being detected, $C_{i,t}$, was conditional upon the individual being alive at sampling period t and in region k . If $A_{i,t}$ was 0 then the $C_{i,t}$ was 0; an animal which was dead cannot be recovered. If $A_{i,t}$ was 1, then

$$C_{i,t} = \theta_{k,i,t} * r_k \quad 4.5$$

where $\theta_{k,i,t}$ was the probability of recovering an individual i in region k in time period t and r_k was the reporting rate in region k . Reporting rates were fixed. The probability of recovering an individual θ in each region k is a function of the instantaneous fishing mortality rate F in region k at age a :

$$\theta_k = 1 - e^{-F_{k,a}} \quad 4.6$$

Fishing mortality at age was estimated as independent parameters in order to evaluate if a tagging study could provide enough data to investigate the impacts of the fishery on individual age classes. Previous simulation work has shown that independent age-specific fishing and natural mortality parameters are well estimated from a tagging model, thus convergence was not expected to be a problem (Jiang *et al.*, 2007). The likelihood for the tag recapture data was equal to:

$$L(C_{k,a}|R) = \prod_{i=1}^N \prod_{t=1}^T C_{k,a}^{R_{i,t}} (1 - C_{k,a})^{1-R_{i,t}} \quad 4.7$$

where $C_{k,a}$ was the probability of being recaptured in region k at age a and $R_{i,t}$ was an $i \times t$ matrix indicating whether the individual i was recaptured in the time period t with 1 being recaptured and 0 otherwise.

A “not age-specific” model was also used to analyze the data from the simulation. In this case the model structure was the same except the natural mortality and fishing mortality parameters are constant across age classes. In both models, uninformative lognormal priors were used for natural mortality and fishing mortality. While it would be possible to estimate P , tag shedding, and reporting rate using this model, previous simulation work has shown that these parameters are unable to be accurately estimated

without the addition of external data sources like double tagging or PSAT tagging (Die *et al.*, 2013; Laretta, 2013) and the objective of this work was to determine if it is possible to estimate age-specific mortalities from a conventional tagging study. Therefore, we assumed that these values are known and fixed in order to focus on the parameters of interest. Estimated parameters were compared to the true values used in the simulation to create the data, with the parameters in the not age-specific model compared to the age specific parameters.

The models were run using OpenBUGS version 3.2.2 rev 1063 (Gilks *et al.*, 1994) for at least 25 000 Markov Chain Monte Carlo (MCMC) iterations with a burn in of 5 000 iterations or until convergence was reached, with a thin of 5 to reduce autocorrelation. The convergence of the MCMC to the stationary posterior distribution was evaluated by the Gelman-Rubin diagnostic, based on the ratio of inter-chain variance to intra-chain variance (Gelman and Rubin, 1992) as well as by examining the trace plots of each estimated parameter. Results were analyzed using R 2.15.2 (R Computing Team, 2014; Appendix D).

Results

Using fishing mortalities in line with those reported from the most recent stock assessments and using reporting rates estimated in Chapter Two for the tagging study, the tag return rate for all the three species was 25% for yellowfin tuna, 27% for bigeye tuna, and 31% for skipjack tuna. While these return rates seem high, the return rate for some historical tagging programs in the Atlantic are around 10-30% but can be up to 40-60% which includes tag retention and reporting rates much less than 100%, especially for

older fish (Hallier, 2000; Gaertner *et al.*, 2004). The number of tag returns for age one fish was the smallest, which is to be expected as they were necessarily recovered in the same year they were released and natural mortality rates were highest (**Table 4.3**). The majority of tag returns occurred in regions one and two, regions with higher fishing mortality and more fishing on the younger age classes in the surface fisheries.

The correlation between natural mortality and fishing mortality for all three species was very low for the age-specific models (**Table 4.4**). The not age-specific models had correlations between the parameters but even these correlations are around 10% for skipjack and yellowfin tuna and up to 25% for bigeye tuna.

Yellowfin tuna

Neither tagging model estimated natural mortality nor fishing mortality well (**Table 4.5**). Natural mortality was overestimated for both the Lorenzen age-specific model and the not age-specific model, with exception of the age one fishing mortality for the not-age specific model, which was underestimated (**Figure 4.2**). The natural mortality estimate was less biased when estimated with a Lorenzen curve than ages 4-6+ and more biased than ages 1-2 in the not age-specific model.

Fishing mortality estimates were generally negatively biased for the age-specific model. The not age-specific fishing mortality estimates were more biased than the not-age specific models and had some large positively biased parameters (**Figure 4.2**). Region one age-specific parameters ranged were between 0 and -50% biased while the not age-specific parameters were between -75% and 100% biased. Region two age-specific parameters were unbiased for ages 5 and 6+ but were positively biased, for the not age-specific parameters. Region three had the best results for the age-specific

parameters, with ages 1-3 unbiased. The parameter estimates for the not age-specific model were also better estimated for region three, although they were still more biased than the age-structured parameters. Region four was not estimated well for either model, with very large positive biases for the ages 4-6+ age-specific parameters, and positive biases for all the not age-specific parameters. Parameters for young fish had a smaller coefficient of variance than the oldest aged fish, which had very broad posterior probability distributions.

Bigeye tuna

Parameter estimates were generally more biased for bigeye tuna not age-specific model than the age-specific model (**Table 4.6**). Natural mortality was overestimated for both the Lorenzen age-structured model and the not age-specific model (**Figure 4.4**). Like yellowfin tuna, the age-specific natural mortality estimate was more biased than ages 1-4 and less biased than ages 5-8+ in the not age-specific model.

The age-specific model estimated a much less biased fishing mortality parameter estimates than the not age-specific model. All of the age-specific parameter estimates were less than 100% biased, most were less than 50% biased, and most of the ages 2-5 were less than 25% biased (**Figure 4.5**). The not age-specific estimates had a large range of biases from -50% to over 400% (**Table 4.6**). The older age classes (ages 5-7+) generally had larger variability compared to the younger age classes, except the age one fishing mortality estimates for regions three and four also had a large variability, likely due to fewer age one recoveries.

Skipjack tuna

The Lorenzen age-structured model the not age-specific model produced positively biased fishing mortality parameter estimates for skipjack tuna (**Table 4.7**). Age-specific natural mortality was less biased than ages 4-6+ and more biased than ages 1-2 from the not age-specific model, but both models produced parameter estimates over 100% biased (**Figure 4.6**). Fishing mortality parameters were generally negatively biased for regions one through three in the age-specific model and positively biased in region four. Parameters in regions one through three were also better estimated than those in region four. Most parameter estimates in region four over 100% biased, while all the parameter estimates in regions one through three are less than 100% biased, and most less than 50% biased. The not age-specific model fishing mortality estimates were generally more biased than the age-specific model estimates (**Figure 4.7**) and some had percent biases over 200%.

Discussion

Incorporating age-specific natural mortality did not significantly improved the accuracy of the natural mortality estimate over estimating a not age-specific natural mortality for any of the species. Previous simulation work using a Brownie model had similar biases in the natural mortality estimates, even when fishing mortality estimates were relatively unbiased. They hypothesized that these biases were due to the models being highly parameterized and large correlations between M and F (Polacheck *et al.*, 2006). The high number of parameters may also explain the biases seen in the age-

specific models and the higher correlations between M and F may explain the biases seen in the not age-specific models.

Most fishing mortality estimates were improved by including age-specific parameters. The lower reporting rate in region four clearly causes fishing mortality to be overestimated for all three species while the other three regions had relatively low biases in the parameter estimates. This is important to any tagging study as the reporting rate clearly impacts the fishing mortality parameter estimates. Hillary and Eveson (2014) also found that reporting rate assumption significantly changed the fishing and natural mortality estimates from skipjack tuna tagging data in the Indian Ocean, although the total mortality was relatively robust. This work also suggests that total mortality could be well estimated from tagging data, as our natural mortality parameters were overestimated and fishing mortality parameters were underestimated. Incorporating catch and effort data using an integrated model can reduce the biases in these estimates (Polacheck *et al.*, 2006; Hillary and Eveson, 2014).

Because the total mortality Z on each species is a sum of the fishing and natural mortalities ($Z=F+M$), we would expect significant correlation between the two parameters. However, the highest correlation between F and M was only 25% in the bigeye tuna models. This may be because the two parameters are estimated from different data. Fishing mortality parameters were only estimated from the R matrix, which was a matrix of 0s and 1s describing if the fish was recovered and returned and was fully observed. The natural mortality parameters are estimated from both the observed and unobserved tags, therefore there is significantly more uncertainty in the parameter estimates due to the unobserved individuals, which could explain why fishing

and natural mortality are not as correlated as expected. However, the results offer some important insights for planning and evaluating the results from future tagging programs.

Our model assumes that age class at tagging was known without error and that the length at age was calculated from the growth curve by assuming there is no variation of age at length. In reality, the majority of the data from the tagging program will not be aged, and only include length data in the initial release year from those released and in the final year of those recaptured. However, the benefits of using a Bayesian process and including the Lorenzen scaled natural mortality rate are that the estimation model framework would allow for the estimation of the age with uncertainty and account for any variation in length at age within the model from the available length data (Zhang *et al.*, 2009). This uncertainty could be from differences in individual growth rates or measurement error in the length measurements. Including variation in growth parameters between individuals would allow for unbiased estimates of the population growth curve. Furthermore, if an aging study was included in the tagging program where the growth model parameters are estimated from an analysis of hard parts, these data could be included in the model to allow for the simultaneous estimation of the growth equation with the mortality estimates (Catalano and Allen, 2010). This would allow for the use of this model in fisheries where the fishing mortality rates among fish of the same age may be different due to the size-selectivity of the fishery which is not currently accounted for in age-specific models.

For yellowfin tuna, allowing natural mortality to be estimated with an age specific parameter based upon a Lorenzen-scaled reference M significantly improved the parameter estimate for the oldest age classes. This shows that the tagging data on

recovered fish contain enough information to estimate the underlying age structure, that when ignored, results in significantly biased parameter estimates, especially for those which have lower tag returns overall. The improved fishing mortality estimates in the age-structured model over the single-parameter model indicated that the age-structure was an important feature of the tagging model, and was significant enough that the model can estimate many of the age-specific parameters well even when they are assumed to be independent parameters. The relatively poor mortality estimates mortalities for age one fish are the result of the relatively few tag returns, probably due to the higher natural mortality and fishing mortalities of age one fish. This suggests that in order to estimate mortalities for all ages well, the tags should be released so that the youngest fish have a slightly higher number of releases, ensuring enough tags are released to be recaptured in the first year and in subsequent years from fish tagged at age one because there are more fish remaining at large. The simulation releases equal numbers of tags for each of the first four age classes, so it may be useful to evaluate a simulation where the number of tags released in each age class is proportional to the total mortality with more tags placed on younger fish. Evaluating how the proportion of tagged fish in each age class may impact the ability to accurately estimate age-specific parameters could be important future work for providing additional recommendations to the design of the AOTTP.

The other parameter estimates were informed both by older tagged fish recaptured in the first year of release and tagged fish from younger age classes being recaptured after at least a year at liberty. Key to this method of tagging to be successful is to ensure that there are consistently long term recoveries. This may be a challenge for the AOTTP to overcome because over 80% of the tags released in historical Atlantic tagging programs

are recaptured in the first few months post release (Ortiz, 2016). One potential solution for ensuring long term recoveries could be to tag fish in areas with low fishing effort in addition to areas with higher fishing effort or to tag fish during periods of low fishing effort. Hallier (2005) found that when tagging within the Dakar fishing area, tags which were released from January to May had higher times at liberty than those released in July through December. July through December was also a period of high fishing effort when 70% of the annual catch was made. This would require more time and effort from the tagging operations as these are probably areas or time periods of lower abundance or more cryptic abundance.

Since the fishing mortality estimates were improved when estimated as age-specific parameters, age-structure should be included when analyzing yellowfin tag returns from the Atlantic Ocean Tuna Tagging Program. The various gears used in the yellowfin fishery have significant age/size selectivity rather than targeting the entire population. The longline fishery targets large adult yellowfin almost exclusively, the baitboat fishery targets small juvenile yellowfin almost exclusively, and the purse seine fishery targets small juvenile yellowfin under FADs and adult yellowfin in free schools (Anonymous, 2011). These fisheries are also fairly localized, where baitboat catch occurs primarily in the Eastern Atlantic, purse seine catch occurs primarily in the Eastern Tropical Atlantic and off the coast of Brazil, and the longline fishery occurs throughout the entire Atlantic. This makes the use of the four region model with different fishing mortality estimates useful because we could take into account the differing catch at age in each region.

For bigeye tuna, including age-specific fishing mortality parameters significantly improved the estimate over the not age-specific model. The well estimated fishing mortality parameters may be because bigeye tuna have the smallest natural mortality rate which allow for more fish to survive to the next age class and be recovered. Since 27% of the tags are recovered, there is enough information to estimate age-specific parameters. These recovery rates are higher than those expected from the AOTTP, since the Indian Ocean tagging program had recovery rates around 15% (Carruthers *et al.*, 2014), but possible in the Atlantic Ocean, where tagging studies have return rates between 7-31% (Hallier, 2000; Fisch, 2005). Also, the reporting rate assumptions significantly changes the number of tags expected and the resulting fishing mortality estimates. Reporting rates can be fleet or even vessel specific, but on average the surface fisheries have historically had reporting rates between 80-90% and the longline fishery has had reporting rates <40% (Carruthers *et al.*, 2014). Since the majority of the tags returned in the Atlantic are expected to come from tuna caught in the purse seine and baitboat fleets, the reporting rates in regions one through three are expected for yellowfin tuna, skipjack tuna, and juvenile bigeye tuna. However, since this is an age structured model, it is important to note that the reporting rates for older yellowfin tuna and especially adult bigeye tuna would be much smaller thus we would expect fewer returns in the oldest age classes caught on longlines, similar to the reporting rates in region four. Since natural mortality was estimated as a function of age, fewer returns from the oldest age classes would likely have a minimal impact on the parameter estimates. Fishing mortality was estimated as independent parameters, therefore the reduction in the number of adult returns would significantly impact the parameter estimates as observed in region four with the

positively biased and poorly estimated fishing mortalities. Using a function to estimate fishing mortality, however, would reduce this impact and may be useful future research.

The range of fishing mortalities used to simulate the bigeye tuna data was large allowing for the model to differentiate between the fishing mortality for each age class. The model may be able to produce well estimated age-specific fishing mortality parameters because the input values are different enough to allow the model to differentiate between them. Whenever the age-specific model is run with age-specific fishing mortalities which were all within 0.05-0.25, the model does not estimate unbiased parameters (results not shown).

Skipjack is perhaps the least likely to benefit from age-structured fishing mortality parameter estimates because skipjack are not caught by longline vessels except as occasional bycatch and are caught at all ages in the surface fisheries. However, the model results showed that the fishing mortality estimates were improved by the age-specific model. The range of age-specific fishing mortalities used to populate the tagging simulation was large, however, so the model was able to differentiate between the different ages.

The comparison between the age structured model and a not age-specific model shows that when the fishery is significantly age structured, such as the tropical tuna fisheries in general, a model with age specific fishing mortality generally produces less biased parameter estimates and reporting rates play an important role in providing unbiased fishing mortality parameter estimates. However, a fully age structured model may not be necessary and a tagging model may be able to account for the different selectivities of the gears with fewer parameters than those used here. Ensuring that the

true F parameters were different for each age allowed the model to estimate them independently, when within region age-parameters are too similar the model produced worse parameter estimates because the model was over parameterized. This means that unless we are sure each age has a different fishing mortality, we should perhaps parameterize the model so that we are estimating parameters that reflect the true fishing pressure. For example for bigeye two fishing mortality parameters may be appropriate, one for the surface fisheries and one for the longline fisheries might produce more accurate fishing mortality estimates than a fully age structured model while still accounting for the changed targeting by gear with age. The surface gears, purse seiners and baitboats, catch almost exclusively juvenile bigeye tuna, until they reach approximately three years of age. The longline vessels catch adult bigeye tuna over the age of three (ICCAT, 2013). Using gear specific fishing mortality rates and grouping bigeye into two classes, juvenile and adult fish, when estimating parameters from the tagging model would still allow the model to capture the change in targeting between the surface gears and the longline gear while estimating fewer parameters than the fully age structured models.

It is possible that an age structured fishing mortality isn't necessary for skipjack tuna because they are targeted by the surface fisheries at all ages and caught only as bycatch in the longline fisheries. It might be useful to use two different fishing mortalities for FAD caught and free school skipjack catches, as the free schools tend to be older individuals and FAD schools tend to be made up of young individuals. For yellowfin tuna, an age structured fishing mortality might be best because the changes between different fleets are more gradual and tend to overlap, with both purse seiner and

longliners catching adult fish and both baitboat and purse seiners catching young fish. Fishery specific or FAD and free school specific fishing mortalities probably would not account for all the heterogeneity in selectivity yellowfin tuna experiences as it grows between different fisheries. Using gear specific or school targeting specific fishing mortalities would reduce the number of parameters estimated while maintaining the heterogeneity observed in the size-selectivity of the three gears for the three tropical tunas.

The biases observed in the estimates of fishing and natural mortality were surprising because the model does produce unbiased estimates of a single parameter when all other parameters are fixed. This means that model is not structurally biased. However, The model does produce relatively unbiased total mortality estimates, which is expected from a tagging model (Hillary and Eveson, 2014). Other work estimating age-specific mortality parameters using catch data and/or tagging data have had trouble estimating age-specific natural mortality well, even when fishing mortality was accurate. Clark (1999) found that using an erroneous natural mortality rate in a stock assessment model resulted in biased fishing mortality estimates, but age-specific selectivity could still be estimated well. Other results suggest it is possible to separate the elements of natural and fishing mortality, however Aanes *et al.* (2007) had difficulties estimating the absolute value of natural mortality in their simulations using catch-at-age data. Many have recommended the use of an integrated model to use both tagging data and catch at age data to estimate the mortality parameters (Polacheck *et al.*, 2006). The catch-at-age

data would necessarily be calculated for each region and the tagging data would be able to be used to estimate movement rates as it is used in many other integrated models (Hulson *et al.*, 2011).

Tropical tuna stock assessments have historically had few spatial components incorporated into the model structure (Anonymous, 2014b; Anonymous, 2016b). Recently, as scientists have recognized that these spatial components are an important part of tropical tuna population dynamics, attempts have been made to use spatially explicit models like Stock Synthesis 3 in the assessments. The most recent bigeye tuna stock assessment used a three region model with the Atlantic Ocean divided into north, south, and central regions to reflect the “primary” central region with the highest catches and dominated by catch from the surface fisheries, and the north and south regions which are primarily longline fleets and have much smaller annual catches (Anonymous, 2016c). Tagging data was not used to estimate movements between these regions because they did not accurately describe movements between the three regions, primarily due to the lack of tagging in the south region (Anonymous, 2016c). Further, analyses of catch data show that there are significant differences in the catch composition of the surface fisheries targeting all three tropical tunas in the Eastern Atlantic (Fonteneau *et al.*, 2000a). Some of these differences can be attributed to fleets using different techniques in these areas such as cooperative FAD fishing in the Gulf of Guinea where baitboats and purse seiners cooperate to catch a school of fish associated with a FAD (Anonymous, 2016b) compared to the technique used by baitboats in Senegal where the boat serves as a FAD and maintains a school of fish associated with it (Hallier and Delgado de Molina, 2000). Some of these differences can also be attributed to the physiological and

biological differences between the three species which drive their annual movements and ontogenetic changes in habitat use such as the movement of bigeye tuna from the surface to the thermocline when they reach maturity (ICCAT, 2013). The estimation model showed that region- and age-specific fishing mortalities are estimable from tagging data. Instead of estimating a single fishing mortality for each stock, estimating region-specific fishing mortalities could identify regions where fishing effort should be decreased to reduce overfishing, or areas where fishing effort could be increased without overfishing the stock. This could allow for a more regional management of the stock including evaluating the effectiveness of marine closures (Sippel *et al.*, 2015), such as the two month closure to FAD fishing of an area of the Gulf of Guinea (Miller and Andersen, 2008; Anonymous, 2016a).

The model described above shows that age-specific parameters are likely an important feature of tagging models and can be estimated with reasonable accuracy, even when they are treated as independent parameters with a space-state model. Incorporating a functional relationship between the age-specific natural mortalities for each species results in a fairly accurate parameter estimate for at least yellowfin and skipjack tuna, and increases the precision of the parameter estimates. It is likely that a similar effect on precision would be expected if a functional relationship was used for fishing mortality such as a selectivity curve, or if fishing mortality was specified based upon the structure of the fisheries, which would also reduce the number of parameters estimated. Based upon the model results, it is recommended that the AOTTP strive to tag fish of all sizes in order to ensure that the change in fishing mortality as the fish ages is captured in the subsequent data analysis. Strategies should be discussed to reduce the number of short-

term recaptures, including not tagging only during periods of high fishing effort where there is a high probability of a short term recovery (Hallier, 2005), and tagging within fishing area closures (Anonymous, 2016a) which are already implemented in the Gulf of Guinea and areas where fishing effort has historically been low. This is to ensure the data are informative enough to estimate the parameters related to the complexity inherent in the Atlantic tropical tuna fisheries.

Table 4.1. Parameters used to simulate a tagging study for yellowfin, skipjack, and bigeye tuna.

Yellowfin		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+		
M		1.7	1.0	0.81	0.70	0.64	0.60		
F	Region 1	0.15	0.25	0.35	0.5	0.65	0.75		
	Region 2	0.75	0.65	0.5	0.35	0.25	0.15		
	Region 3	0.45	0.4	0.35	0.3	0.25	0.2		
	Region 4	0.2	0.25	0.3	0.35	0.4	0.45		
Proportion Tagged		0.2	0.2	0.2	0.2	0.1	0.1		
P		Region 1	Region 2	Region 3	Region 4				
		Region 1	0.948	0.05	0.001	0.001			
		Region 2	0.05	0.6	0.15	0.2			
		Region 3	0.001	0.15	0.799	0.05			
		Region 4	0.001	0.2	0.05	0.749			
Reporting Rate	0.8		0.9	0.8	0.4				
Age-Length Function	$Length_{age} = 192.4(1 - \exp^{-0.37(age+0.003)})$					Draganik and Pelczarski (1984)			
Bigeye		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8+
M		0.68	0.44	0.35	0.30	0.26	0.24	0.23	0.21
F	Region 1	0.5	0.4	0.3	0.1	0.2	0.3	0.4	0.45
	Region 2	0.5	0.45	0.4	0.3	0.25	0.2	0.15	0.1
	Region 3	0.05	0.05	0.1	0.25	0.3	0.35	0.4	0.45
	Region 4	0.05	0.1	0.15	0.2	0.25	0.3	0.4	0.45
		0.15	0.15	0.15	0.15	0.1	0.1	0.1	0.1

Proportion Tagged							
P		Region 1	Region 2	Region 3	Region 4		
	Region 1	0.749	0.2	0.001	0.05		
	Region 2	0.2	0.65	0.05	0.1		
	Region 3	0.001	0.05	0.749	0.2		
	Region 4	0.05	0.1	0.2	0.65		
Reporting Rate		0.8	0.9	0.8	0.4		
Age-Length Function	$Length_{age} = 217.3(1 - \exp^{-0.18(age+0.709)})$				Hallier <i>et al.</i> (2004)		
Skipjack							
		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
M		1.8	1.0	0.75	0.63	0.55	0.51
F	Region 1	0.3	0.4	0.7	0.8	0.8	0.9
	Region 2	0.5	0.8	1	0.8	0.5	0.4
	Region 3	0.1	0.4	0.6	0.9	0.9	1
	Region 4	0.1	0.2	0.3	0.2	0.1	0.1
Proportion Tagged		0.2	0.2	0.2	0.2	0.1	0.1
P		Region 1	Region 2	Region 3	Region 4		
	Region 1	0.848	0.15	0.001	0.001		
	Region 2	0.15	0.839	0.01	0.001		
	Region 3	0.001	0.01	0.889	0.1		
	Region 4	0.001	0.001	0.1	0.898		
Reporting Rate		0.8	0.9	0.8	0.4		
Age-Length Function	$Length_{age} = 97.3(1 - \exp^{-0.251(age)})$				Hallier and Gaertner (2006)		

Table 4.2. List of indices, model variables, data, and model parameters used for this analysis.

Symbol	Description
Indices	
N	Number of tags released
T	Number of time periods
i	Individual
t	time period
f	Cohort
k, l	Regions
a	Age-class
Data	
A_{i,t}	Indicator if the individual <i>i</i> is alive (1) or dead (0), unobserved (NA) in time period <i>t</i>
R_{i,t}	Indicator if the individual <i>i</i> is returned (1) or not (0) in time period <i>t</i>
m_{i,t}	Location of individual <i>i</i> in time period <i>t</i> , 1-4 if observed, NA if not
Model Parameters	
S_{i,t}	Probability of survival for individual <i>i</i> in time period <i>t</i>
C_{i,t}	Probability of detection for individual <i>i</i> in time period <i>t</i>
θ_{i,t}	Probability of recapture for individual <i>i</i> in time period <i>t</i>
M_a	Instantaneous fishing mortality at age <i>a</i>
M_r	Instantaneous fishing mortality at the reference age <i>r</i>
L_r	Length at reference age <i>r</i>
L_a	Length at age
F_{k,a}	Instantaneous fishing mortality in region <i>k</i> at age <i>a</i>
r_k	Reporting Rate in region <i>k</i>
P_{k,l}	Annual movement rate from region <i>k</i> to region <i>l</i>

Table 4.3. Number of tag returns for each species by age and region.

Yellowfin Tuna					
Age	Region				Grand Total
	1	2	3	4	
1	170	508	320	198	1196
2	336	584	397	330	1647
3	491	570	408	424	1893
4	648	434	423	558	2063
5	384	194	185	336	1099
6+	410	137	181	392	1120
Grand Total	2439	2427	1914	2238	9018
				Percent Returned	25%

Bigeye Tuna					
Age	Region				Grand Total
	1	2	3	4	
1	610	678	156	93	1537
2	547	752	237	148	1684
3	441	699	445	267	1852
4	460	639	620	350	2069
5	172	129	171	104	576
6	169	102	195	100	566
7	240	81	233	127	681
8+	252	76	224	152	704
Grand Total	2891	3156	2281	1341	9669
				Percent Returned	27%

Skipjack Tuna					
Age	Region				Grand Total
	1	2	3	4	
0	238	414	140	131	923
1	507	692	488	283	1970
2	731	891	727	378	2727
3	770	856	929	289	2844
4	459	338	485	119	1401
5+	471	311	538	114	1434
Grand Total	3176	3502	3307	1314	11299
				Percent Returned	31%

Table 4.4. Correlation matrix between natural mortality and fishing mortality parameters for the Lorenzen Models and the Not age-specific Models for each species.

[region, age]	Lorenzen M Models			Not age-specific Models			
	YFT M_r	BET M_r	SKJ M_r	YFT M	BET M	SKJ M	
F at age[1,1]	-0.0008	0.029	-0.009	F Region 1	0.130	0.248	0.078
F at age[1,2]	0.003	0.012	-0.035	F Region 2	0.078	0.156	0.102
F at age[1,3]	-0.005	-0.032	-0.031	F Region 3	0.124	0.228	0.099
F at age[1,4]	-0.008	0.034	0.037	F Region 4	0.118	0.100	0.107
F at age[2,1]	0.016	0.052	0.052				
F at age[2,2]	0.032	-0.018	0.025				
F at age[2,3]	0.031	0.040	-0.003				
F at age[2,4]	-0.007	0.009	-0.015				
F at age[3,1]	0.042	0.063	0.055				
F at age[3,2]	0.021	0.054	0.010				
F at age[3,3]	0.038	0.020	0.041				
F at age[3,4]	0.021	0.056	0.040				
F at age[4,1]	0.034	0.029	0.018				
F at age[4,2]	0.037	0.039	0.064				
F at age[4,3]	0.057	0.060	0.046				
F at age[4,4]	0.019	0.065	0.020				
F at age[5,1]	0.077	0.079	0.066				
F at age[5,2]	0.072	0.088	0.062				
F at age[5,3]	0.047	0.114	0.018				
F at age[5,4]	0.070	0.133	0.071				
F at age[6,1]	0.074	0.087	0.028				
F at age[6,2]	0.070	0.096	0.032				
F at age[6,3]	0.058	0.087	0.019				
F at age[6,4]	0.037	0.096	0.087				
F at age[7,1]		0.075					
F at age[7,2]		0.061					
F at age[7,3]		0.069					
F at age[7,4]		0.077					
F at age[8,1]		0.057					
F at age[8,2]		0.014					
F at age[8,3]		0.040					
F at age[8,4]		0.055					

Table 4.5. Estimated parameters from the yellowfin tuna space state models. The age structured parameter values from the simulation model (actual) were used to estimate the percent bias for both the age-specific and the not-age-specific space state model.

Parameter	Actual Value	Estimated Mean	Mean Percent Bias	CV	
Age specific parameters					
F Region 1	Age 1	0.15	0.08	-81%	0.10
	Age 2	0.25	0.17	-78%	0.06
	Age 3	0.35	0.27	-61%	0.05
	Age 4	0.5	0.36	44%	0.05
	Age 5	0.65	0.54	-57%	0.05
	Age 6+	0.75	0.59	-41%	0.05
F Region 2	Age 1	0.75	0.33	-34%	0.06
	Age 2	0.65	0.40	-55%	0.05
	Age 3	0.5	0.37	-39%	0.05
	Age 4	0.35	0.27	-95%	0.06
	Age 5	0.25	0.24	-84%	0.07
	Age 6+	0.15	0.15	-80%	0.09
F Region 3	Age 1	0.2	0.20	-67%	0.06
	Age 2	0.25	0.25	-72%	0.06
	Age 3	0.3	0.27	-45%	0.05
	Age 4	0.35	0.23	-70%	0.06
	Age 5	0.4	0.22	-86%	0.07
	Age 6+	0.45	0.19	-61%	0.08
F Region 4	Age 1	0.45	0.24	-66%	0.09
	Age 2	0.4	0.41	-49%	0.07
	Age 3	0.35	0.50	26%	0.07
	Age 4	0.3	0.72	-28%	0.06
	Age 5	0.25	0.95	-24%	0.08
	Age 6+	0.2	1.46	485%	0.11
Lorenzen Reference					
M		0.54	0.98	82%	0.01
Not Age Specific Parameters					
M	Age 1	1.74	1.44	-17%	0.01
	Age 2	1.03	1.44	40%	0.01
	Age 3	0.81	1.44	78%	0.01
	Age 4	0.70	1.44	106%	0.01
	Age 5	0.64	1.44	125%	0.01
	Age 6+	0.61	1.44	136%	0.01

F region 1	Age 1	0.15	0.29	-27%	0.02
	Age 2	0.25	0.29	-63%	0.02
	Age 3	0.35	0.29	-58%	0.02
	Age 4	0.5	0.29	17%	0.02
	Age 5	0.65	0.29	-77%	0.02
	Age 6+	0.75	0.29	-71%	0.02
F region 2	Age 1	0.75	0.30	-40%	0.03
	Age 2	0.65	0.30	-67%	0.03
	Age 3	0.5	0.30	-50%	0.03
	Age 4	0.35	0.30	-94%	0.03
	Age 5	0.25	0.30	-80%	0.03
	Age 6+	0.15	0.30	-60%	0.03
F region 3	Age 1	0.2	0.23	-62%	0.03
	Age 2	0.25	0.23	-75%	0.03
	Age 3	0.3	0.23	-54%	0.03
	Age 4	0.35	0.23	-70%	0.03
	Age 5	0.4	0.23	-85%	0.03
	Age 6+	0.45	0.23	-54%	0.03
F region 4	Age 1	0.45	0.62	-11%	0.03
	Age 2	0.4	0.62	-22%	0.03
	Age 3	0.35	0.62	56%	0.03
	Age 4	0.3	0.62	-38%	0.03
	Age 5	0.25	0.62	-50%	0.03
	Age 6+	0.2	0.62	149%	0.03

Table 4.6. Estimated parameters from the bigeye tuna space state models. The age structured parameter values from the simulation model (actual) were used to estimate the percent bias for both the age-specific and the not-age-specific space state model.

Parameter	Actual Value	Estimated Mean	Mean Percent Bias	CV	
Age specific parameters					
F Region 1	Age 1	0.5	0.37	-26%	0.05
	Age 2	0.4	0.35	-12%	0.05
	Age 3	0.3	0.27	-11%	0.05
	Age 4	0.1	0.11	5%	0.07
	Age 5	0.2	0.25	24%	0.06
	Age 6	0.3	0.39	31%	0.07
	Age 7	0.4	0.52	31%	0.07
	Age 8+	0.45	0.53	18%	0.07
F Region 2	Age 1	0.5	0.32	-37%	0.05
	Age 2	0.45	0.39	-14%	0.05
	Age 3	0.4	0.40	-1%	0.05
	Age 4	0.3	0.32	8%	0.05
	Age 5	0.25	0.34	38%	0.06
	Age 6	0.2	0.33	63%	0.07
	Age 7	0.15	0.21	39%	0.09
	Age 8+	0.1	0.16	56%	0.10
F Region 3	Age 1	0.05	0.06	16%	0.11
	Age 2	0.05	0.06	26%	0.09
	Age 3	0.1	0.11	7%	0.07
	Age 4	0.25	0.28	11%	0.05
	Age 5	0.3	0.41	37%	0.06
	Age 6	0.35	0.47	35%	0.07
	Age 7	0.4	0.49	22%	0.07
	Age 8+	0.45	0.47	5%	0.07
F Region 4	Age 1	0.05	0.10	97%	0.12
	Age 2	0.1	0.13	26%	0.10
	Age 3	0.15	0.22	44%	0.08
	Age 4	0.2	0.31	54%	0.07
	Age 5	0.25	0.41	63%	0.08
	Age 6	0.3	0.46	54%	0.10
	Age 7	0.4	0.63	57%	0.10
	Age 8+	0.45	0.61	35%	0.10
Lorenzen Reference M	0.17	0.57	235%	0.01	

Not Age Specific Parameters					
M	Age 1	0.70	0.84	20%	0.01
	Age 2	0.44	0.84	69%	0.01
	Age 3	0.35	0.84	111%	0.01
	Age 4	0.30	0.84	141%	0.01
	Age 5	0.26	0.84	181%	0.01
	Age 6	0.24	0.84	212%	0.01
	Age 7	0.23	0.84	237%	0.01
	Age 8+	0.21	0.84	301%	0.01
F region 1	Age 1	0.5	0.28	-43%	0.02
	Age 2	0.4	0.28	-29%	0.02
	Age 3	0.3	0.28	-5%	0.02
	Age 4	0.1	0.28	185%	0.02
	Age 5	0.2	0.28	42%	0.02
	Age 6	0.3	0.28	-5%	0.02
	Age 7	0.4	0.28	-29%	0.02
	Age 8+	0.45	0.28	-37%	0.02
F region 2	Age 1	0.5	0.32	-36%	0.03
	Age 2	0.45	0.32	-29%	0.03
	Age 3	0.4	0.32	-20%	0.03
	Age 4	0.3	0.32	7%	0.03
	Age 5	0.25	0.32	28%	0.0
	Age 6	0.2	0.32	60%	0.03
	Age 7	0.15	0.32	113%	0.03
	Age 8+	0.1	0.32	220%	0.03
F region 3	Age 1	0.05	0.20	308%	0.03
	Age 2	0.05	0.20	308%	0.03
	Age 3	0.1	0.20	104%	0.03
	Age 4	0.25	0.20	-18%	0.03
	Age 5	0.3	0.20	-32%	0.03
	Age 6	0.35	0.20	-42%	0.03
	Age 7	0.4	0.20	-49%	0.03
	Age 8+	0.45	0.20	-55%	0.03
F region 4	Age 1	0.05	0.26	420%	0.04
	Age 2	0.1	0.26	160%	0.04
	Age 3	0.15	0.26	73%	0.04
	Age 4	0.2	0.26	30%	0.04
	Age 5	0.25	0.26	4%	0.04
	Age 6	0.3	0.26	-13%	0.04
	Age 7	0.4	0.26	-35%	0.04
	Age 8+	0.45	0.26	-42%	0.04

Table 4.7. Estimated parameters from the skipjack tuna space state models. The age structured parameter values from the simulation model (actual) were used to estimate the percent bias for both the age-specific and the not-age-specific space state model.

Parameter	Actual Value	Estimated Mean	Mean Percent Bias	CV	
Age Specific Parameters					
F Region 1	Age 1	0.3	0.13	-57%	0.009
	Age 2	0.4	0.27	-31%	0.02
	Age 3	0.7	0.55	-21%	0.02
	Age 4	0.8	0.55	-31%	0.02
	Age 5	0.8	0.64	-20%	0.03
	Age 6+	0.9	0.71	-21%	0.04
F Region 2	Age 1	0.5	0.24	-52%	0.01
	Age 2	0.8	0.44	-45%	0.02
	Age 3	1	0.68	-32%	0.03
	Age 4	0.8	0.56	-30%	0.02
	Age 5	0.5	0.43	-15%	0.02
	Age 6+	0.4	0.33	-17%	0.02
F Region 3	Age 1	0.1	0.04	-57%	0.006
	Age 2	0.4	0.29	-27%	0.02
	Age 3	0.6	0.45	-26%	0.02
	Age 4	0.9	0.70	-22%	0.03
	Age 5	0.9	0.75	-16%	0.04
	Age 6+	1	0.78	-22%	0.04
F Region 4	Age 1	0.1	0.13	27%	0.01
	Age 2	0.2	0.31	53%	0.03
	Age 3	0.3	0.63	112%	0.04
	Age 4	0.2	0.47	137%	0.06
	Age 5	0.1	0.29	185%	0.03
	Age 6+	0.1	0.27	170%	0.03
Lorenzen Reference M	0.4	0.85	112%	0.009	
Not Age Structured Parameters					
M	Age 1	0.3	1.55	-14%	0.01
	Age 2	0.4	1.55	53%	0.01
	Age 3	0.7	1.55	105%	0.01
	Age 4	0.8	1.55	146%	0.01
	Age 5	0.8	1.55	177%	0.01
	Age 6+	0.9	1.55	202%	0.01

F region 1	Age 1	0.3	0.43	42%	0.02
	Age 2	0.4	0.43	6%	0.02
	Age 3	0.7	0.43	-39%	0.02
	Age 4	0.8	0.43	-47%	0.02
	Age 5	0.8	0.43	-47%	0.02
	Age 6+	0.9	0.43	-53%	0.02
F region 2	Age 1	0.5	0.45	-9%	0.02
	Age 2	0.8	0.45	-43%	0.02
	Age 3	1	0.45	-55%	0.02
	Age 4	0.8	0.45	-43%	0.02
	Age 5	0.5	0.45	-9%	0.02
	Age 6+	0.4	0.45	13%	0.02
F region 3	Age 1	0.1	0.43	333%	0.02
	Age 2	0.4	0.43	8%	0.02
	Age 3	0.6	0.43	-28%	0.02
	Age 4	0.9	0.43	-52%	0.02
	Age 5	0.9	0.43	-52%	0.02
	Age 6+	1	0.43	-57%	0.02
F region 4	Age 1	0.1	0.36	260%	0.03
	Age 2	0.2	0.36	80%	0.03
	Age 3	0.3	0.36	20%	0.03
	Age 4	0.2	0.36	80%	0.03
	Age 5	0.1	0.36	260%	0.03
	Age 6+	0.1	0.36	260%	0.03

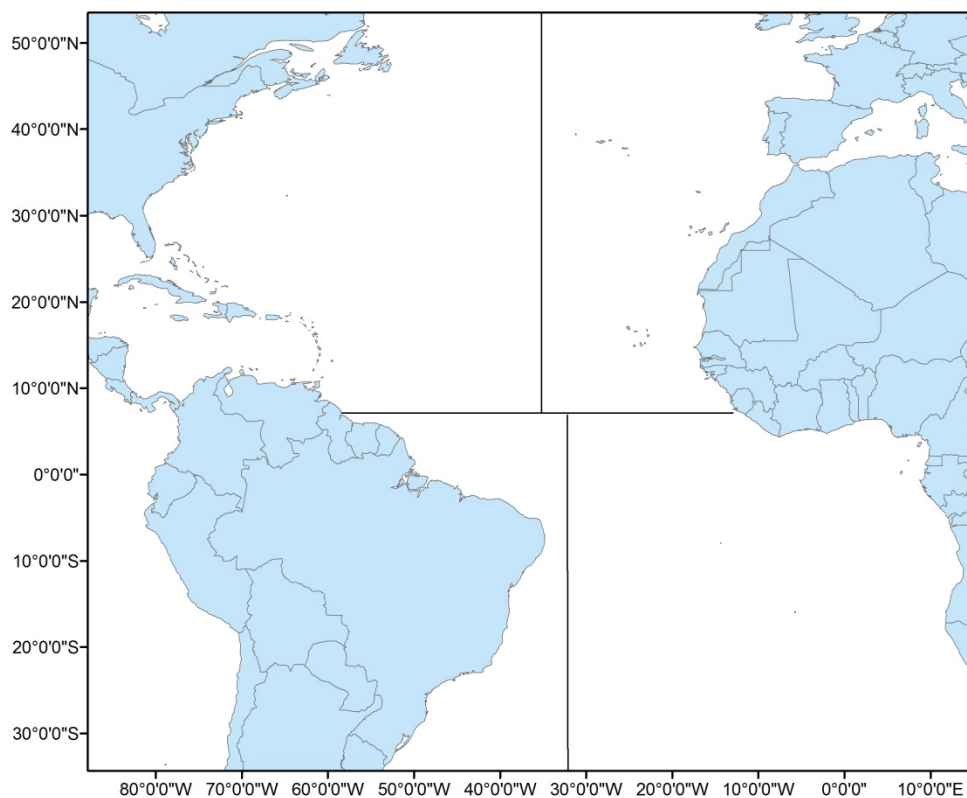


Figure 4.1. Four region model used with region one the northeast Atlantic, region two the southeast Atlantic, region three the southwest Atlantic, and region four the northwest Atlantic.

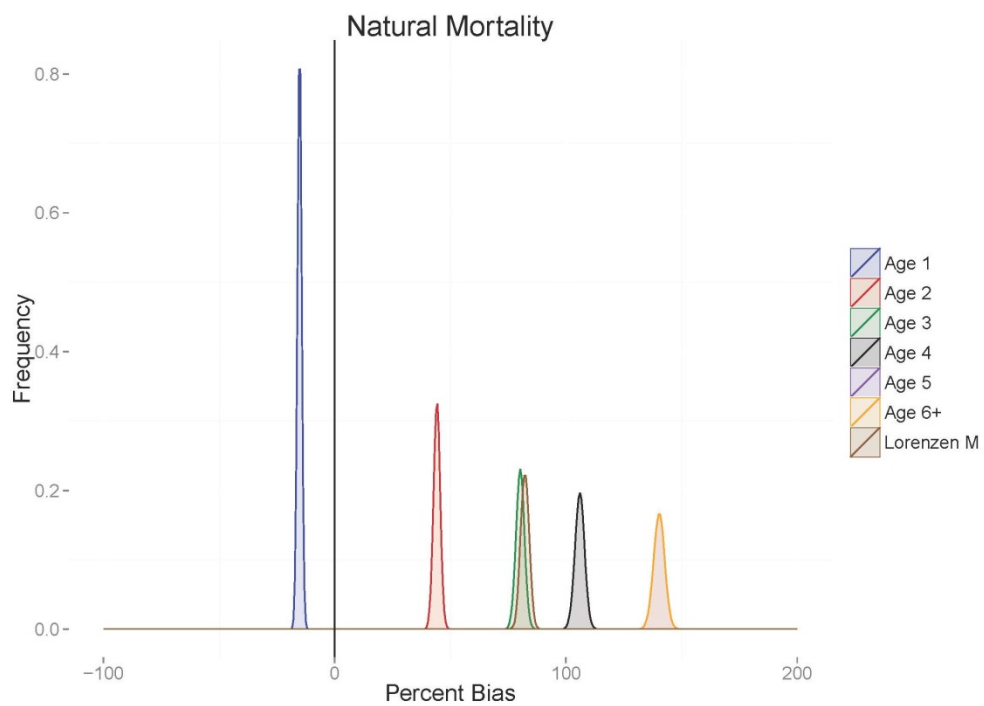


Figure 4.2. Posterior distributions of yellowfin tuna natural mortality as percent bias compared to the true parameter. Black line indicates 0% bias.

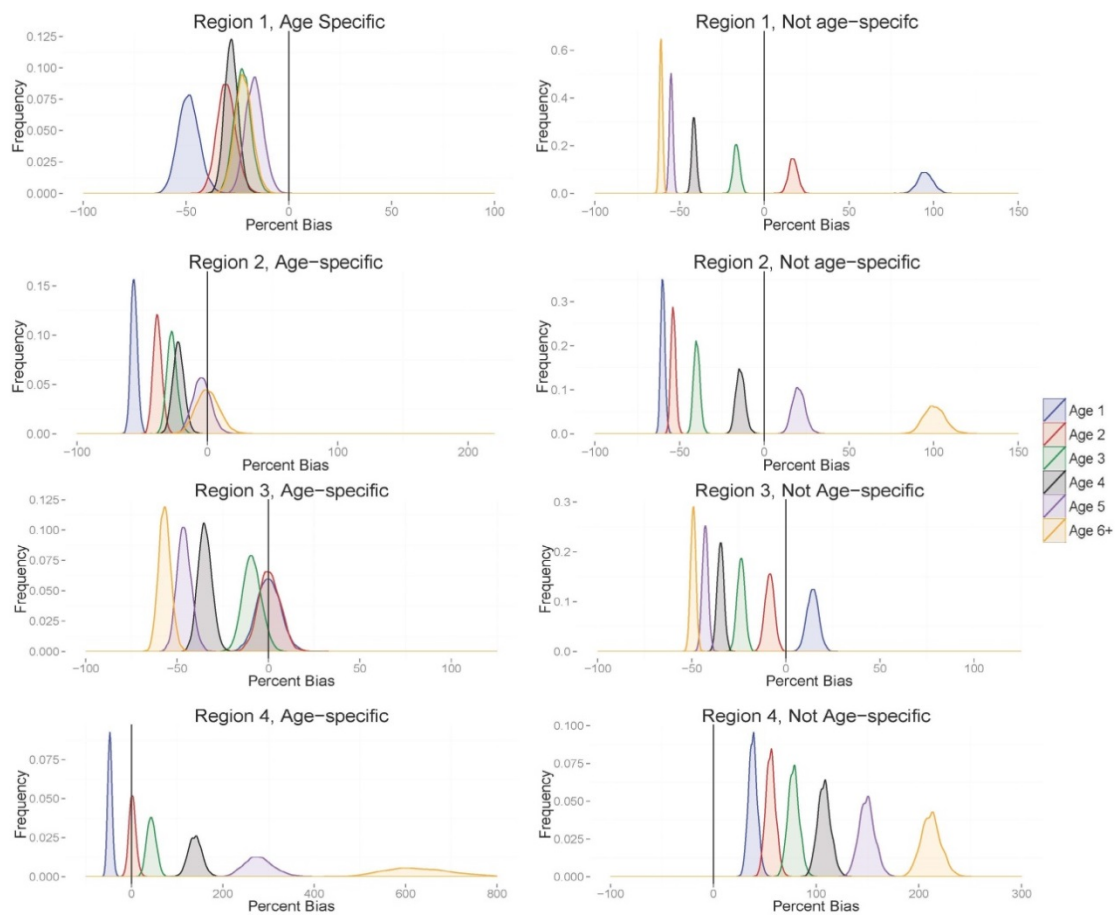


Figure 4.3. Posterior distribution of yellowfin tuna age- and region- specific fishing mortality as percent bias compared to the true parameter. Black line indicates 0% bias.

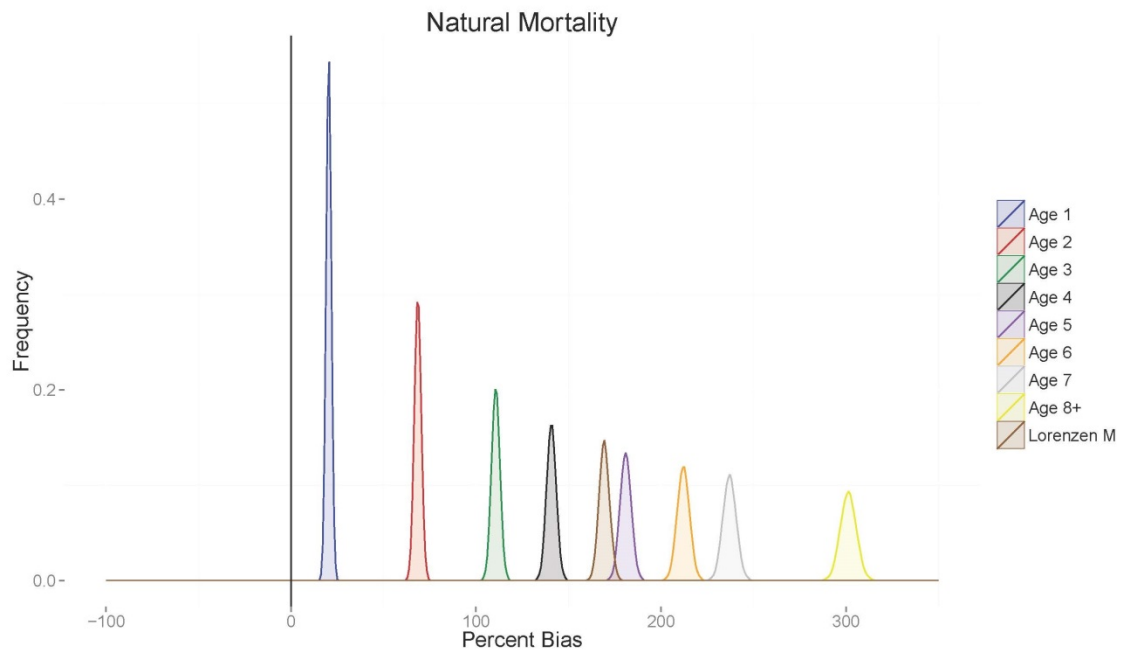


Figure 4.4. Posterior distributions of bigeye tuna natural mortality as percent bias compared to the true parameters. Black line indicates 0% bias.

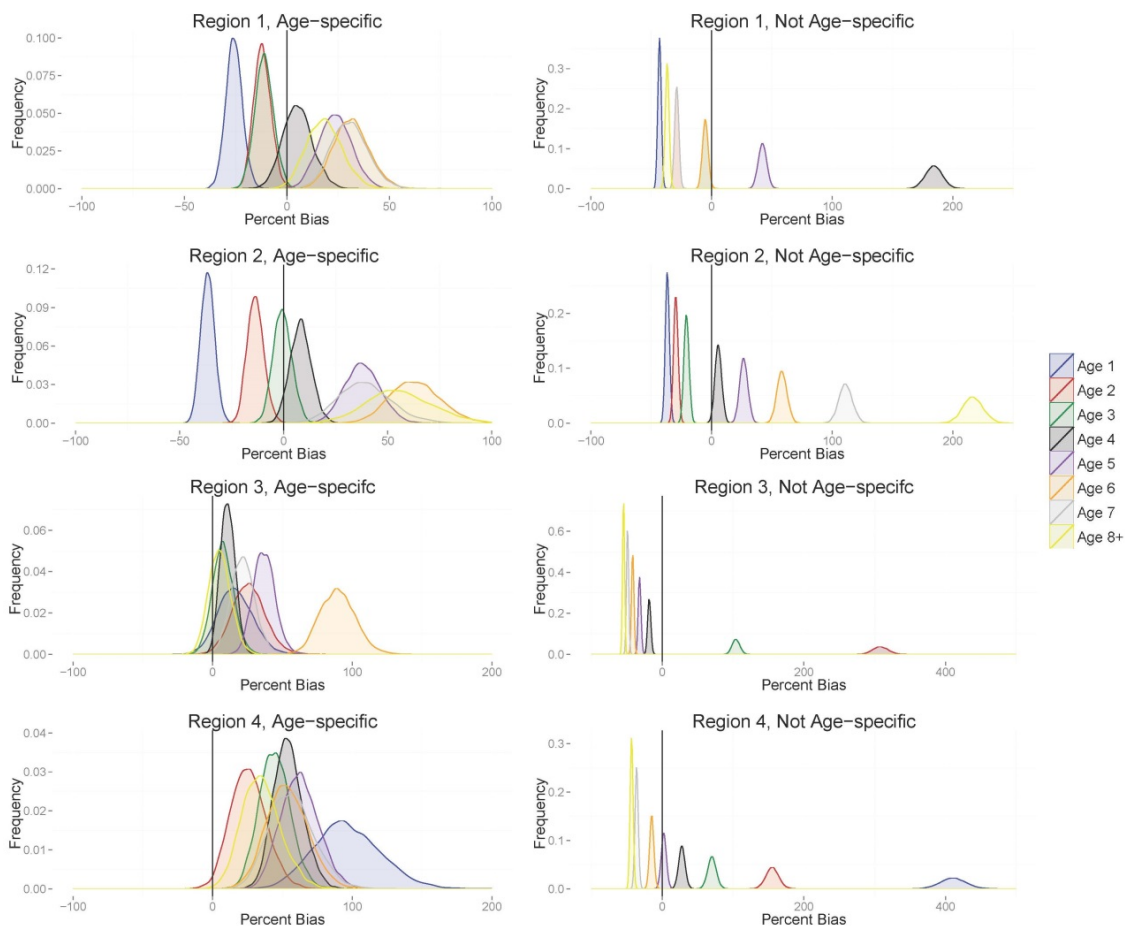


Figure 4.5. Posterior distribution of bigeye tuna age- and region- specific fishing mortality as percent bias compared to the true parameter. Black line indicates 0% bias.

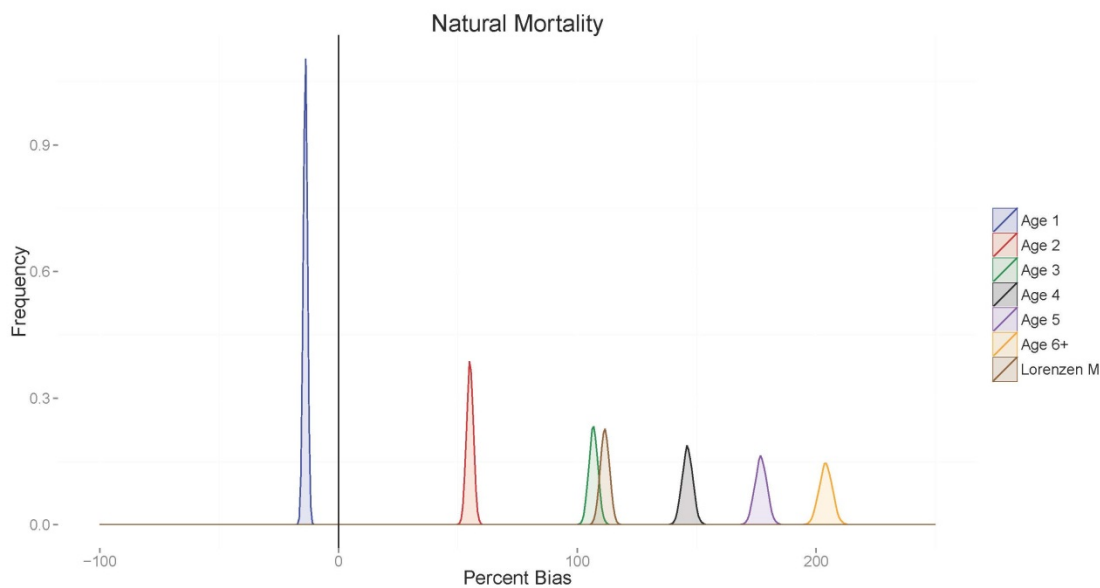


Figure 4.6. Posterior distributions of skipjack tuna natural mortality as percent bias compared to the true parameters. Black line indicates 0% bias.

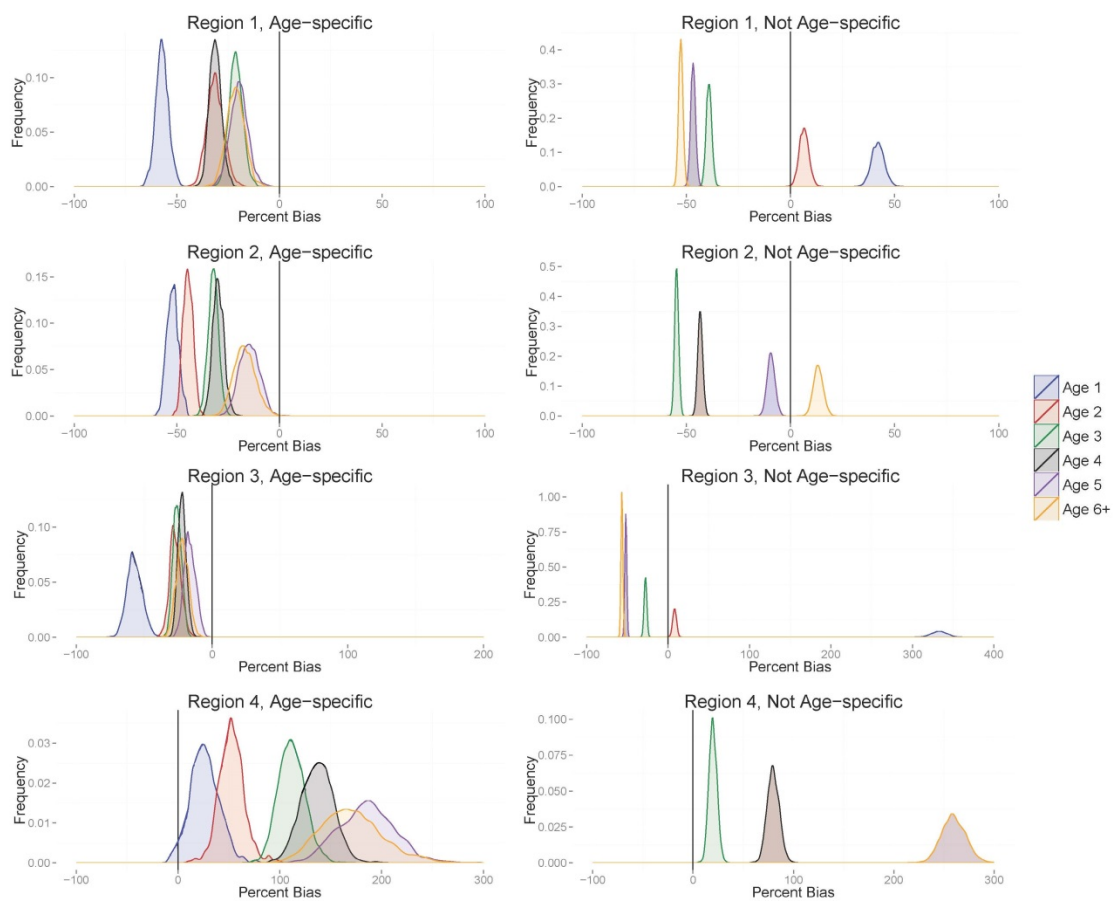


Figure 4.7. Posterior distribution of skipjack tuna age- and region- specific fishing mortality as percent bias compared to the true parameter. Black line indicates 0% bias.

CHAPTER 5: SYNTHESIS, RECOMMENDATIONS, AND CONCLUSIONS

Large-scale tagging programs can provide a wealth of fishery independent data on important life history parameters such as growth, maturity, stock structure, movement rates, fishing mortality and natural mortality. These parameters are necessary and valuable inputs to stock assessment models and when they are not known precisely they lead to highly uncertain assessments of stock status. This uncertainty makes providing management advice challenging, and led to the development of the Atlantic Ocean Tuna Tagging Program (AOTTP). The AOTTP provides an excellent opportunity to collect tagging data from the relatively data-poor Atlantic tropical tuna stocks. To help ensure that the AOTTP meets its goals and is successful we have used, as proposed by Leroy *et al.*, 2015 a simulation model to test various tagging design scenarios and to evaluate the performance of different types of tags. The large tagging programs in the Pacific and Indian Oceans as well as the small tagging programs in the Atlantic Ocean, were used to parameterize the simulations enhancing the probability that simulated populations are a reasonable approximation for reality.

Analysis of Historical Tagging Data

The analysis of historical tagging data showed there was not enough data to estimate basin-wide movement rates from the four regions used in chapters three and four, with the Atlantic divided east and west at 32°W and north and south at 7°N, primarily due to the concentration of tags in the eastern Atlantic with few release and recapture events in the western Atlantic. This analysis highlighted the necessity of tagging fish throughout the entire Atlantic, rather than in localized areas. Furthermore,

the majority of the data were from short-term recoveries which provide information on the area-specific parameters such as the local fishing mortality but are limited in their use for estimating stock-wide parameters. However, the analysis provided quantitative movement rates within the Eastern Atlantic estimated from the tagging data which supported the previous hypotheses about tropical tuna movements. Previous hypotheses indicate tropical tuna movements north out of the Gulf of Guinea in the spring and a return to the Gulf in the fall, along with seasonal east and west movements by yellowfin from the Caribbean Sea to the Gulf of Guinea for reproduction (Miyabe and Bard, 1986; Hallier *et al.*, 2004; Zagalia *et al.*, 2004; Hallier, 2005; Carruthers *et al.*, 2010). The CPUE data analysis provided information of the seasonal movement of the three species into the northwestern Atlantic over the course of the boreal summer. These movements are likely driven in part by their response to the changes in water temperature (Graham, 1974; Brill, 1994; Brill and Lutcavage, 2001) and their response to prey movements, as they are known to be fairly opportunistic predators (Lebourges-Dhaussy *et al.*, 2000; Menard *et al.*, 2006).

The movement rates estimated by the tagging model and described by the CPUE data suggest that significant exchange occurs between regions within the eastern Atlantic Ocean, movements that should be taken into account whenever the stocks are assessed, as many of the baitboat and purse seine fleets targeting tropical tunas are localized and employ different targeting techniques (Fonteneau *et al.*, 2000a). The incorporation of spatially explicit assessment models into tropical tuna stock assessments has begun

(Anonymous, 2016c), and the results of the AOTTP is seen as a necessary step in obtaining parameter estimates on the stock structure which can help support the development of these models (Million, 2013).

Recommendations for the AOTTP

The simulation work for the AOTTP provided many insights on what kind of information is necessary to have a successful tagging program where the data can be used to estimate fishing and natural mortality and stock structure and movement rates. Previous research with this simulation showed that releasing conventional tags equally between regions produces the least biased fishing and natural mortality parameter estimates (Die *et al.*, 2013; Laretta, 2013). The analysis of historical tag data, concentrated in the eastern Atlantic showed that basin-wide movement rate estimates require tag releases and recoveries to occur in all regions. The recommendation for the AOTTP is to distribute tagging efforts throughout the Atlantic dispersing tags as equally as possible. This ensures parameter estimates reflect the entire population or stock, rather than the regions where the majority of the tags are released.

The analysis of the historical tagging data and the parameterization of the simulation framework required the development of priors for use in the Bayesian estimation models. Using a meta-analysis of historical Atlantic tagging programs and incorporating parameters estimated from tagging studies in the Indian and Pacific Oceans, instantaneous tag shedding rate and tag reporting rate priors were developed. It is recommended that these informative priors be used when analyzing the tagging data from the AOTTP.

The electronic tagging simulation showed that the fishing and natural mortality parameter estimates are very similar to each other, with the DST tags producing better parameter estimates in regions where there are large movement rates and low residency rates but PSAT tags performing better in areas with low reporting rates. The biggest disadvantages for using popup satellite archival tags (PSAT) are that only large fish can be tagged and PSATs are rarely at large for more than a year (Musyl *et al.*, 2011; Thorstad *et al.*, 2013; Jepsen *et al.*, 2015). Movement rates estimated from these tags only apply to large tuna and do not provide information on juvenile movements. The short time at large for PSAT tags means that the movement information is limited. These tags are best suited for habitat studies, bycatch survival, handling mortality from tagging, and short term movements when there is low chance of DST returns rather than long-term movement studies (Cooke *et al.*, 2013a).

Data storage tags, however are well adapted to long term studies as tag loss is generally low, data can be retrieved even if the batteries die, and DSTs typically have a much longer time at liberty (Ådlandsvik *et al.*, 2007; Thorstad *et al.*, 2013; Jepsen *et al.*, 2015). The biggest disadvantage to DSTs is that recoveries are dependent upon returns from the fishery. This means that more tags must be released to achieve high enough return rates to provide sufficient data on movements. There is also a risk of bias if tag return rates vary in ways that are not adequately incorporated into the estimation model. However, the model results indicate that even when return rates are similar to those expected from conventional tags, movement rates are estimable from the data and provide good estimates of fishing and natural mortality parameters. These return rates are within the expected range of return rates from conventional tags and DSTs

(Hallier, 2000; Block *et al.*, 2005; Schaefer *et al.*, 2007; Walli *et al.*, 2009; Whitlock *et al.*, 2012; Teo *et al.*, 2013). The best way to ensure tags are returned when they are caught is to implement a well-planned publicity and recovery campaign (Million, 2013). This type of campaign should be implemented in all areas where tropical tuna caught in the Atlantic are expected to be landed. Since this is necessary for the recovery of conventional tags, the additional information regarding DSTs will not be an undue burden to the tagging program and will significantly increase the probability of tags being returned. Therefore it is recommended that the AOTTP use DSTs to provide information on movements and stock structure and ensure that the publicity campaign for the AOTTP include information on how to return DSTs. A combination of PSAT and DST tags may eliminate the concerns about low reporting rates, however it is unknown if the reduced number of each electronic tag released would impact the parameter estimates.

The age-structured simulation addressed questions about potential problems with the tagging platform proposed for the AOTTP. Tagging operations will primarily occur on baitboat vessels, from which large numbers of tropical tunas have been successfully tagged in other tagging programs (Hallier and Fonteneau, 2015), although the majority of the fish tagged will be small and/or juveniles. This simulation showed that when the underlying tagged population experiences age-specific fishing and natural mortality, modeling these parameters assuming constant fishing and natural mortality across ages produces significantly biased parameter estimates. This is an important consideration for the AOTTP because a goal of the program is to estimate population parameters for the entire population. Therefore the recommendation to the AOTTP is to selectively tag individuals based upon their size and ensure that tags are distributed across all sizes.

Key to both obtaining good estimates of movement rates from DSTs and estimating age-specific mortality parameters is reducing the number of short-term recoveries in favor of long times at large for the tags. This is particularly challenging for the AOTTP because historically 80% of conventional tags released have been recovered within the first few months (Ortiz, 2016). Two methods to reduce the number of short-term recoveries are 1.) tag during periods of low fishing effort or 2.) tag in area with low fishing effort. Hallier (2005) found that tags released outside the main Dakar fishing season, July-December, which accounts for over 70% of the annual catch, had much longer times at liberty than those released during their fishing season. Additionally, a two month closure in the Gulf of Guinea FAD fishery (Anonymous, 2016a) would provide opportunities for tagging tuna while fishing effort is low. Tagging fish outside of the main fishing regions would contribute to aiding in ensuring tags are distributed throughout the Atlantic and potentially increase the time at liberty for those tagged individuals.

Future Research

This research was the first attempt at analyzing the historical Atlantic tropical tagging data to provide Bayesian priors for movement rates, tag shedding rates, and reporting rates for tropical tunas. The simulation modeling also provided a significant amount of insight to the AOTTP to help ensure the program is successful. All of the data in this research were modeled using an annual time step, with the exception of the electronic tag data. However, the analysis of the historical tagging and catch data suggested that the tropical tunas make important seasonal movements that cannot be

captured in the annual time step. It would be useful to use a seasonal or monthly time step in future analyses of the data collected from the AOTTP to fully understand these movements. This type of analysis was not possible using the historical tagging data as it was too sparse for a more frequent time step, however due to the scale of the AOTTP, it is probable that a seasonal time step would be possible using the data collected.

One of the most significant advantages to using the Bayesian space-state model to analyze tagging data was that individual heterogeneity can be incorporated into the survival and detection probabilities (Gimenez *et al.*, 2007; Royle, 2008). In the simulation work described here, the individual heterogeneity was the age of the fish, which was assumed to be known without error. However, in the AOTTP the age of the fish will only be available for those fish which are aged using hard parts, and length data will be collected for the releases and the majority of the recoveries. This model framework already incorporates a growth curve to calculate the age-specific natural mortality, and incorporating individual length data rather than age data would be relatively simple. This would allow for the uncertainty around the individual length measurements and the variability around the growth curve to be incorporated into the tagging model to estimate the age-specific mortality parameters (Royle, 2009). The AOTTP intends to collect hard parts to age the tropical tunas, this data could also be incorporated into the tagging model. This would allow for inclusions of uncertainty in the aging process and allow for a growth model to be developed with individual variegation within the growth model parameters (Zhang *et al.*, 2009; Lunn *et al.*, 2013). All of these additions to the current estimation model framework will help ensure that the

population parameters estimated from the Atlantic Ocean Tuna Tagging Program accurately reflect the tropical tuna stocks and reduce uncertainty in future stock assessments.

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APPENDIX A: ADDITIONAL TABLES AND DIAGNOSTIC PLOTS FOR THE HISTORICAL TAG DATA ANALYSIS

Table A1. Movement and residency rates, fishing mortality, and tag shedding rates and the coefficient of variation (CV) for each of the mortality rate assumptions used the bigeye tuna models. First numbers of the movement rates indicate origin and final numbers indicate destination. Azores = 1, Canary Islands = 2, Senegal/Cape Verde Islands = 3, North Sherbro = 4, Sherbro = 5, Cote d’Ivoire = 6, Cape Lopez =7, Equatorial = 8.

	Mean	CV		Mean	CV		Mean	CV
F	0.25	9%	p[3,5]	0.01	123%	p[6,3]	0.10	101%
M	0.80	0.4%	p[3,6]	0.01	121%	p[6,4]	0.11	103%
lambda	0.01	182%	p[3,7]	0.05	57%	p[6,5]	0.08	110%
p[1,1]	0.12	91%	p[3,8]	0.02	113%	p[6,6]	0.36	45%
p[1,2]	0.15	85%	p[4,1]	0.09	97%	p[6,7]	0.09	104%
p[1,3]	0.14	87%	p[4,2]	0.11	89%	p[6,8]	0.08	106%
p[1,4]	0.14	87%	p[4,3]	0.10	91%	p[7,1]	0.08	101%
p[1,5]	0.10	94%	p[4,4]	0.36	42%	p[7,2]	0.12	89%
p[1,6]	0.12	89%	p[4,5]	0.08	96%	p[7,3]	0.11	96%
p[1,7]	0.12	90%	p[4,6]	0.09	96%	p[7,4]	0.12	90%
p[1,8]	0.11	92%	p[4,7]	0.10	92%	p[7,5]	0.07	106%
p[2,1]	0.02	122%	p[4,8]	0.08	95%	p[7,6]	0.10	88%
p[2,2]	0.74	9%	p[5,1]	0.12	91%	p[7,7]	0.19	58%
p[2,3]	0.11	43%	p[5,2]	0.14	87%	p[7,8]	0.21	53%
p[2,4]	0.03	88%	p[5,3]	0.13	87%	p[8,1]	0.07	94%
p[2,5]	0.02	125%	p[5,4]	0.14	86%	p[8,2]	0.08	90%
p[2,6]	0.02	131%	p[5,5]	0.11	90%	p[8,3]	0.08	95%
p[2,7]	0.05	71%	p[5,6]	0.13	88%	p[8,4]	0.08	94%
p[2,8]	0.02	119%	p[5,7]	0.13	87%	p[8,5]	0.07	96%
p[3,1]	0.02	112%	p[5,8]	0.12	90%	p[8,6]	0.07	95%
p[3,2]	0.04	81%	p[6,1]	0.09	106%	p[8,7]	0.34	33%
p[3,3]	0.82	6%	p[6,2]	0.11	95%	p[8,8]	0.21	49%
p[3,4]	0.03	82%						

Table A2. Movement and residency rates, fishing mortality, and tag shedding rates and the coefficient of variation (CV) for each of the mortality rate assumptions used in the skipjack tuna models. First numbers of the movement rates indicate origin and final numbers indicate destination. Canary Islands = 1, Senegal/Cape Verde Islands = 2, North Sherbro = 3, Cote d'Ivoire = 4, Cape Lopez =5, Equatorial = 6.

	Single F		Two Fs		
	Mean	CV	Mean	CV	
F	0.10	1%	F[1]	0.10	1%
M	0.80	1%	F[2]	0.15	1%
lambda	0.79	12%	M	0.80	1%
p[1,1]	0.98	1%	lambda	0.78	13%
p[1,2]	0.01	40%	p[1,1]	0.98	1%
p[1,3]	0.00	0%	p[1,2]	0.01	44%
p[1,4]	0.002	50%	p[1,3]	0.000	0%
p[1,5]	0.002	100%	p[1,4]	0.002	50%
p[1,6]	0.01	38%	p[1,5]	0.002	50%
p[2,1]	0.05	39%	p[1,6]	0.01	43%
p[2,2]	0.92	2%	p[2,1]	0.05	40%
p[2,3]	0.02	29%	p[2,2]	0.93	2%
p[2,4]	0.003	67%	p[2,3]	0.02	30%
p[2,5]	0.001	100%	p[2,4]	0.002	100%
p[2,6]	0.002	100%	p[2,5]	0.001	100%
p[3,1]	0.11	84%	p[2,6]	0.002	100%
p[3,2]	0.23	62%	p[3,1]	0.11	86%
p[3,3]	0.40	32%	p[3,2]	0.24	62%
p[3,4]	0.04	109%	p[3,3]	0.39	32%
p[3,5]	0.06	95%	p[3,4]	0.03	106%
p[3,6]	0.16	56%	p[3,5]	0.06	95%
p[4,1]	0.004	125%	p[3,6]	0.16	55%
p[4,2]	0.02	56%	p[4,1]	0.01	100%
p[4,3]	0.02	46%	p[4,2]	0.02	56%
p[4,4]	0.86	4%	p[4,3]	0.03	50%
p[4,5]	0.04	44%	p[4,4]	0.86	3%
p[4,6]	0.06	39%	p[4,5]	0.04	45%
p[5,1]	0.03	163%	p[4,6]	0.06	38%
p[5,2]	0.004	125%	p[5,1]	0.02	175%
p[5,3]	0.01	71%	p[5,2]	0.003	133%
p[5,4]	0.09	56%	p[5,3]	0.01	67%
p[5,5]	0.65	24%	p[5,4]	0.08	60%
p[5,6]	0.22	61%	p[5,5]	0.68	23%
p[6,1]	0.18	146%	p[5,6]	0.21	68%
p[6,2]	0.01	538%	p[6,1]	0.18	156%

p[6,3]	0.01	100%	p[6,2]	0.01	608%
p[6,4]	0.04	67%	p[6,3]	0.004	100%
p[6,5]	0.52	50%	p[6,4]	0.03	77%
p[6,6]	0.25	76%	p[6,5]	0.53	55%
			p[6,6]	0.24	89%

Table A3. Movement and residency rate, fishing mortality, and tag shedding rates and the coefficient of variation (CV) for each of the mortality rate assumptions for yellowfin tuna models. First number indicates origin and second number indicates destination. NE = 1, SE = 2, W = 3.

	Single F		Multiple Fs	
	Mean	CV	Mean	CV
F	0.17	17%	F[1]	0.224 28%
M	0.41	0.2%	F[2]	0.315 22%
lambda	0.39	19%	F[3]	0.273 22%
p[1,1]	0.92	4%	F[4]	0.206 24%
p[1,2]	0.06	46%	F[5]	0.244 21%
p[1,3]	0.02	78%	F[6]	0.119 26%
p[2,1]	0.08	52%	M	0.408 3%
p[2,2]	0.92	4%	lambda	0.45 15%
p[2,3]	0.002	33%	p[1,1]	0.927 4%
p[3,1]	0.01	78%	p[1,2]	0.056 54%
p[3,2]	0.09	100%	p[1,3]	0.017 82%
p[3,3]	0.90	3%	p[2,1]	0.079 44%
			p[2,2]	0.919 4%
			p[2,3]	0.002 150%
			p[3,1]	0.007 86%
			p[3,2]	0.095 32%
			p[3,3]	0.899 3%

Table A4. Δ AIC values for the five best fit models for each region and species.

Model	Bigeye Tuna							
	Region 1		Region 2		Region 3		Region 4	
	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.
Month	110.85	0	585	9.5	4620	1470	12160	5671
Month + Effort	5.46	0	49	11.8	1130	582	1070	2117
Month + Effort + Fleet	5.46	0	0	18.2	740	446	230	1830
Month + Fleet	5.46	0	12	14.7	1600	1014	880	3066
Month + Gear	5.46	0	77	0	4450	1380	11690	4332
Year + Month	0	11.2	178	13.1	4450	430	11690	3225
Year + Month + Effort	0	11.2	20	17.5	860	169	800	1014
Year + Month + Gear	0	11.2	59	7.5	460	276	920	1107
Year + Month + Fleet	0	11.2	12	12.4	680	117	270	615
Year + Month + Effort + Fleet	0	11.2	0	10.8	490	0	50	536
Year + Month + Effort + Gear	0	11.2	20	14.5	260	171	730	449
Year + Month + Fleet + Gear	0	11.2	5	6.8	250	102	100	42
Year + Month + Effort + Gear + Fleet	0	11.2	0	1256.3	0	0	0	0

Model	Region 5		Region 6		Region 7		Region 8	
	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.
Month	10720	8119	4960	13340	1517	2602	24660	13110
Month + Effort	920	2494	1900	3020	233	1164	1880	2090
Month + Effort + Fleet	630	2327	1290	2610	187	769	630	1505
Month + Fleet	1820	4809	3290	5900	876	1179	3950	6270
Month + Gear	10020	7519	4900	11770	1495	2217	24620	11170
Year + Month	10060	2384	4900	1180	1239	686	1550	2500

Year + Month + Effort	260	610	610	1210	55	602	840	964
Year + Month + Gear	790	906	990	1180	1239	686	1550	2500
Year + Month + Fleet	450	554	1520	1280	260	132	2570	1437
Year + Month + Effort + Fleet	0	123	170	710	0	130	20	144
Year + Month + Effort + Gear	230	535	540	650	9	395	810	835
Year + Month + Fleet + Gear	310	535	270	240	9	0	370	715
Year + Month + Effort + Gear + Fleet	0	0	0	0	0	128	0	0

Skipjack Tuna

Model	Region 1		Region 2		Region 3		Region 4	
	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.
Month	75.9	0	261.8	174	5570	1281	9650	5893
Month + Effort	0	2.0	125.5	58.3	1640	173	1800	827
Month + Effort + Fleet	0	7.8	40	28.3	150	0	60	11
Month + Fleet	0.6	2.0	131.5	68.3	2640	154	1940	493
Month + Gear	0.6	2.0	136.9	67.3	2370	247	1870	936
Year + Month	0	7.8	56	95	3770	1000	8750	5063
Year + Month + Effort	0	7.8	22	0	1380	80	1210	304
Year + Month + Gear	0	7.8	56	48.3	310	65	570	377
Year + Month + Fleet	0	7.8	40	39.2	1300	49	1940	73
Year + Month + Effort + Fleet	0	7.8	0	32.3	1070	14	670	0
Year + Month + Effort + Gear	0	7.8	22	31	230	66	510	298
Year + Month + Fleet + Gear	0.6	2.0	115.4	56.8	1350	68	1160	323
Year + Month + Effort + Gear + Fleet	0	7.8	0	1983.7	0	1	0	3

	Region 5		Region 6		Region 7		Region 8	
	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.
Month	10390	3580	3320	14300	2141	624	21560	10150
Month + Effort	1360	830	1860	3520	507	328	1840	1770
Month + Effort + Fleet	30	10	40	650	31	15	40	10
Month + Fleet	2180	730	1050	3070	662	23	2780	2090
Month + Gear	3050	810	450	7250	1261	37	2650	1550
Year + Month	8600	2890	2410	7890	1411	42	20250	9310
Year + Month + Effort	440	340	1390	2390	190	88	1000	1190
Year + Month + Gear	450	370	180	3310	255	531	1070	780
Year + Month + Fleet	360	360	760	750	33	48	1910	1500
Year + Month + Effort + Fleet	10	30	210	70	0	0	0	100
Year + Month + Effort + Gear	440	280	150	2000	84	5	970	740
Year + Month + Fleet + Gear	870	410	520	1260	309	0	630	370
Year + Month + Effort + Gear + Fleet	0	0	0	0	0	1	0	0

Yellowfin Tuna

Model	Region 1		Region 2		Region 3		Region 4	
	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.
Month	23	0	196.2	28.6	6470	743	20530	976
Month + Effort	0.1	1.97	108.5	15.4	780	587	1310	698
Month + Effort + Fleet	0.1	1.97	61.1	18	590	476	480	584
Month + Fleet	0.1	1.97	93.5	20.4	2690	492	2790	755
Month + Gear	0.1	1.97	92.1	16.4	4330	488	3930	634
Year + Month	0	0	139.5	13.4	4560	390	20070	640
Year + Month + Effort	0	0	86.1	5.7	360	268	720	476

Year + Month + Gear	0	0	69.1	16.1	720	205	630	302
Year + Month + Fleet	0	0	33.4	0	390	233	260	408
Year + Month + Effort + Fleet	0	0	0	1.3	100	205	260	366
Year + Month + Effort + Gear	0	0	66.2	7.6	260	95	390	78
Year + Month + Fleet + Gear	0	0	0.4	2.7	310	18	160	49
Year + Month + Effort + Gear + Fleet	0	0	0	Not Converged	0	0	0	0
	Region 5		Region 6		Region 7		Region 8	
Model	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.	Positives	Prop. Pos.
Month	20920	1611	14820	3380	3590	281	44940	1978
Month + Effort	1200	466	3350	680	700	72	2710	412
Month + Effort + Fleet	590	401	1950	380	188	48	920	203
Month + Fleet	5300	970	6720	1030	850	98	11430	792
Month + Gear	6310	1578	8340	2550	2180	280	9650	1523
Year + Month	19890	350	10710	470	2480	118	42640	850
Year + Month + Effort	390	120	1870	150	375	30	1700	198
Year + Month + Gear	940	323	2380	460	1290	90	2860	698
Year + Month + Fleet	2300	42	4350	230	338	6	7750	263
Year + Month + Effort + Fleet	20	0	710	30	0	0	110	0
Year + Month + Effort + Gear	360	120	360	150	102	32	1370	157
Year + Month + Fleet + Gear	390	45	1170	190	201	2	860	240
Year + Month + Effort + Gear + Fleet	0	2	0	0	0	0	0	4

Diagnostic Plots of the Bayesian Movement models

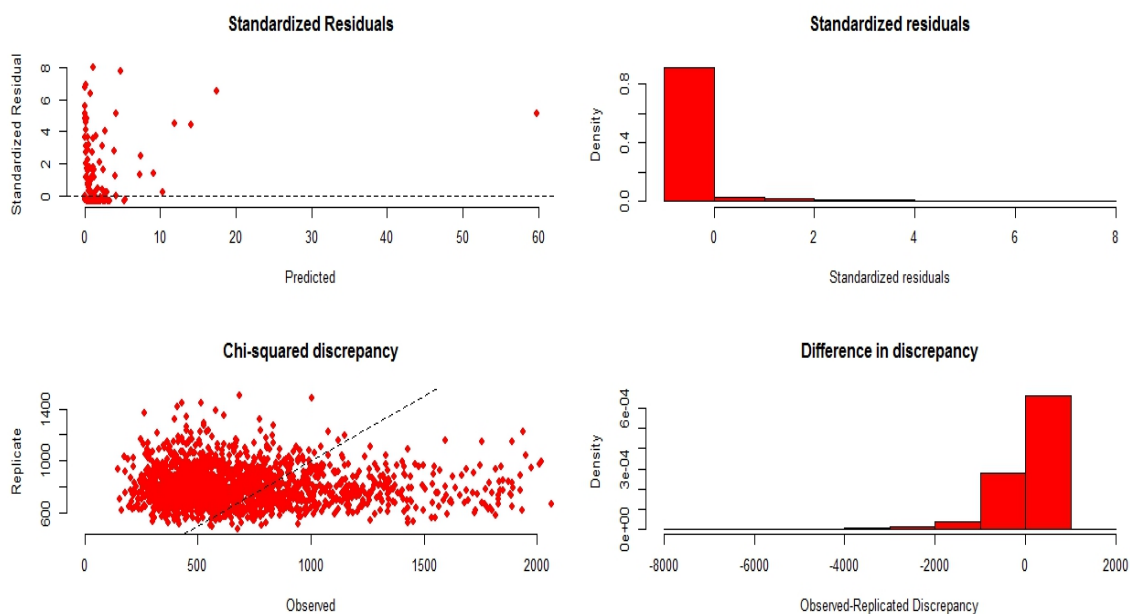


Figure A1. Diagnostic plots for the bigeye tuna model.

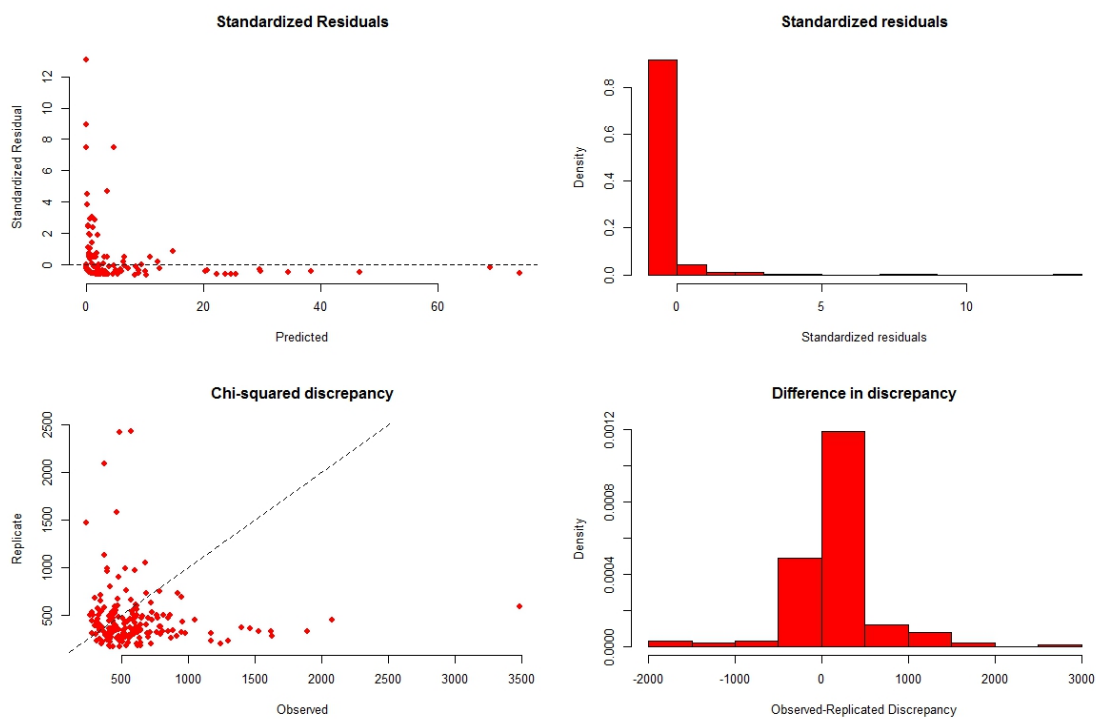


Figure A2. Diagnostic plots for the yellowfin tuna Single F model.

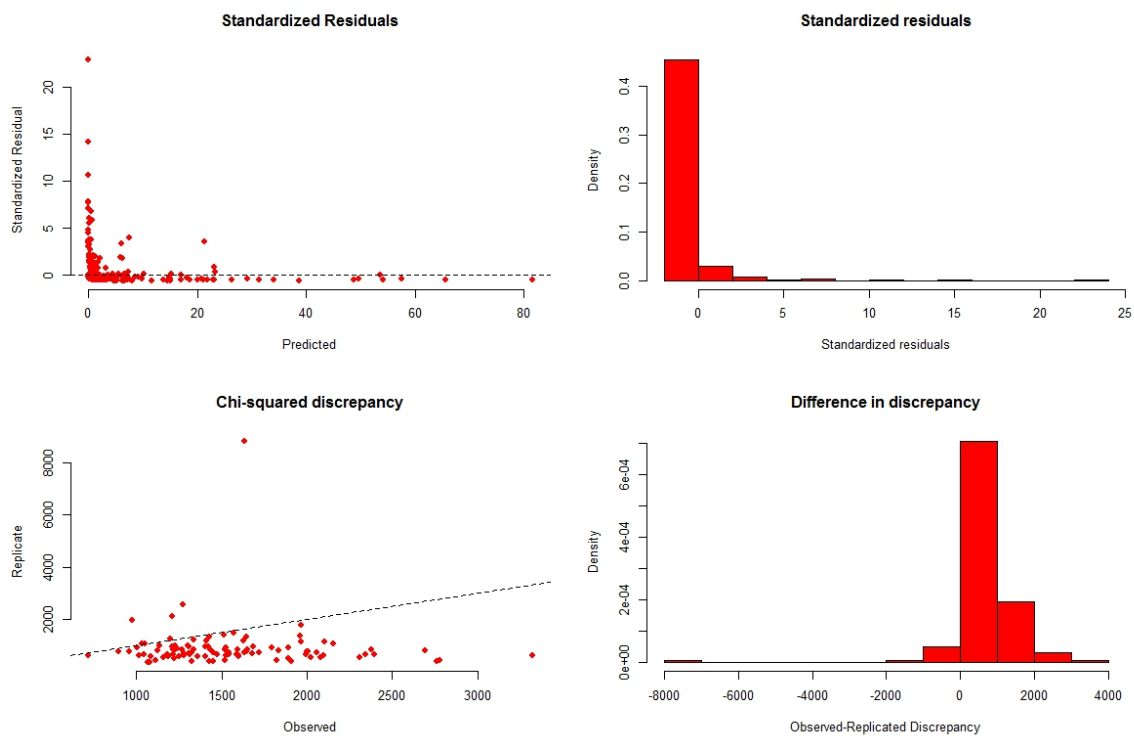


Table A3. Diagnostic plots for the yellowfin tuna multiple F model.

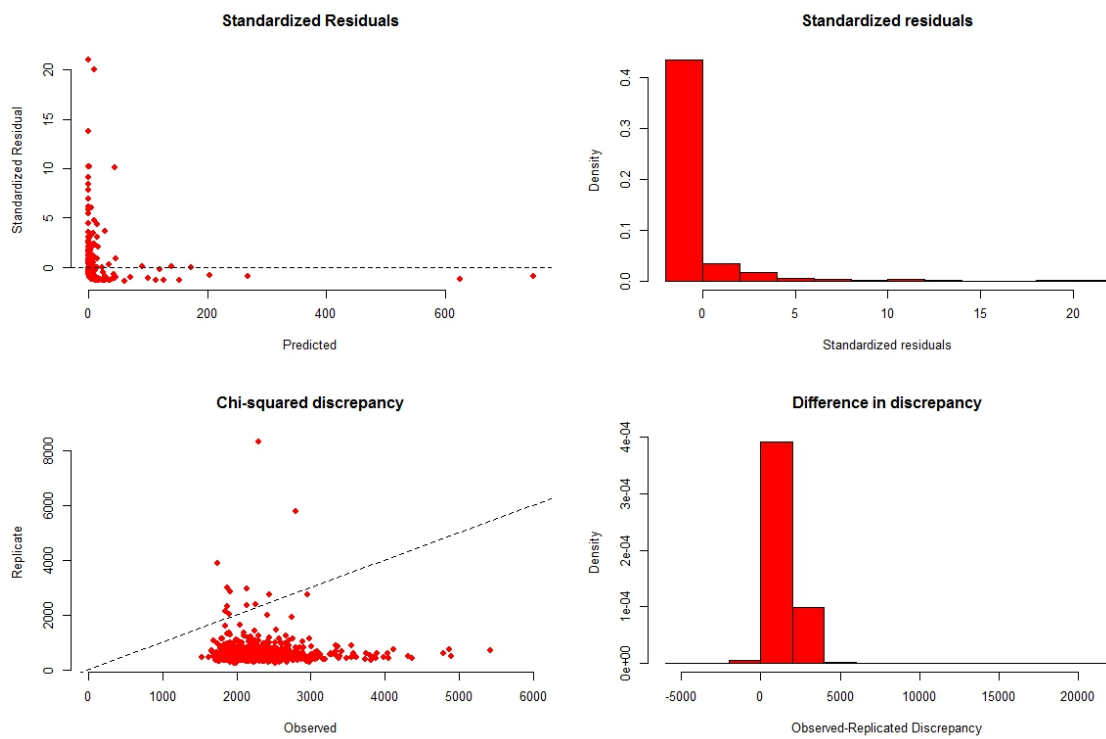


Figure A4. Diagnostic plots for the skipjack tuna Single F model.

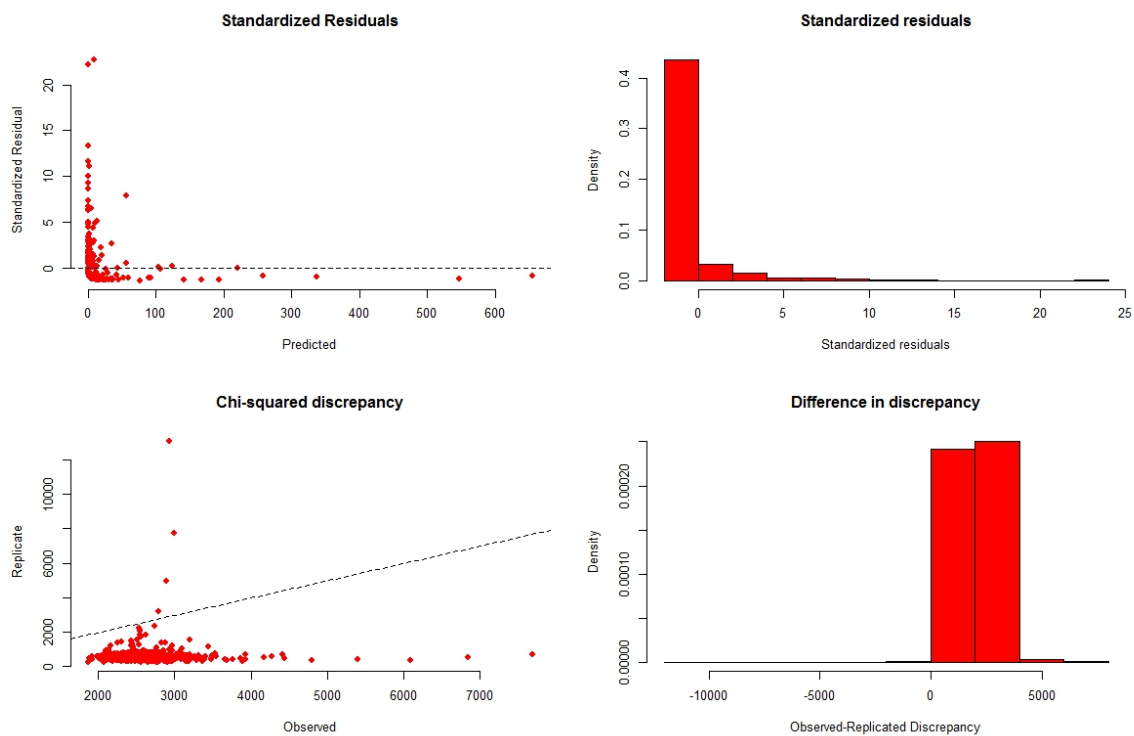


Figure A5. Diagnostic plots for the skipjack tuna Multiple Fs model.

CPUE Model Diagnostics

Bigeye tuna

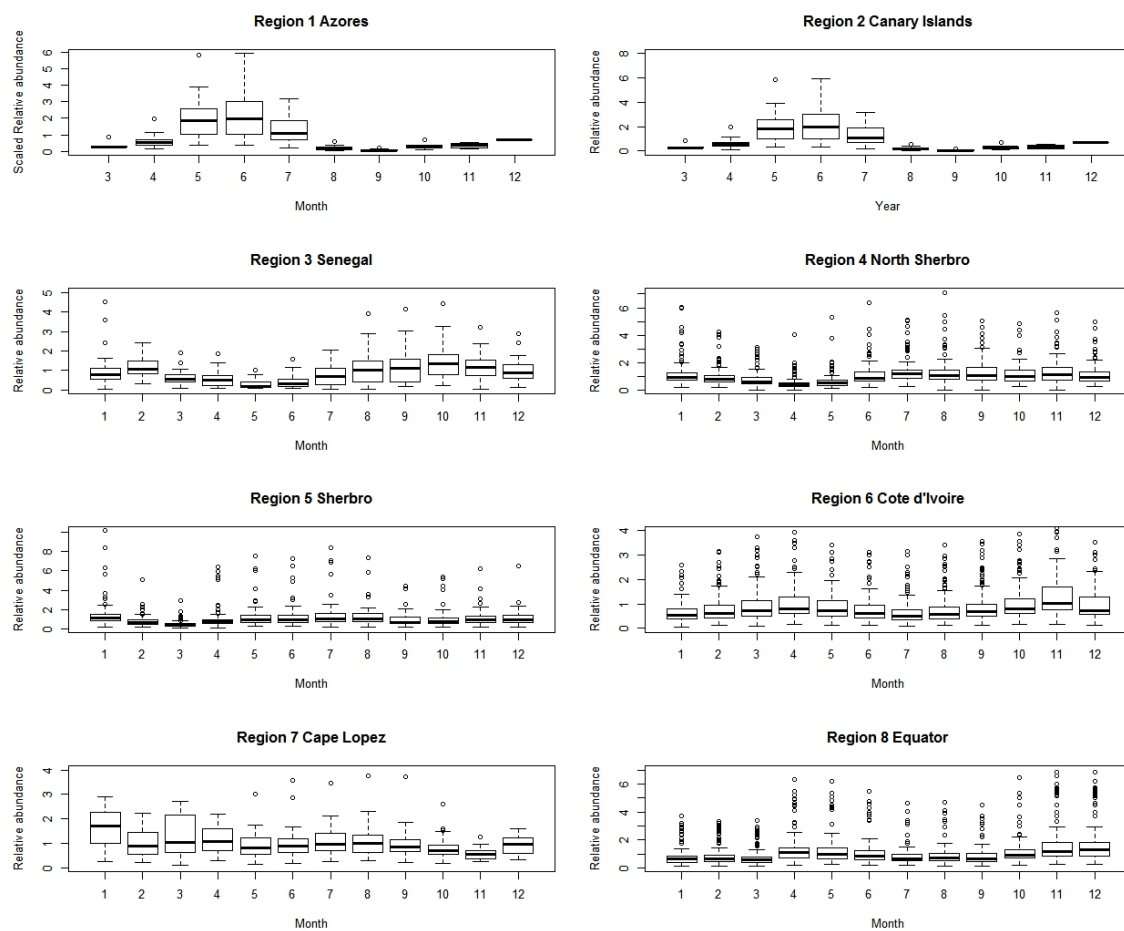


Figure A6. Standardized monthly CPUEs for bigeye tuna.

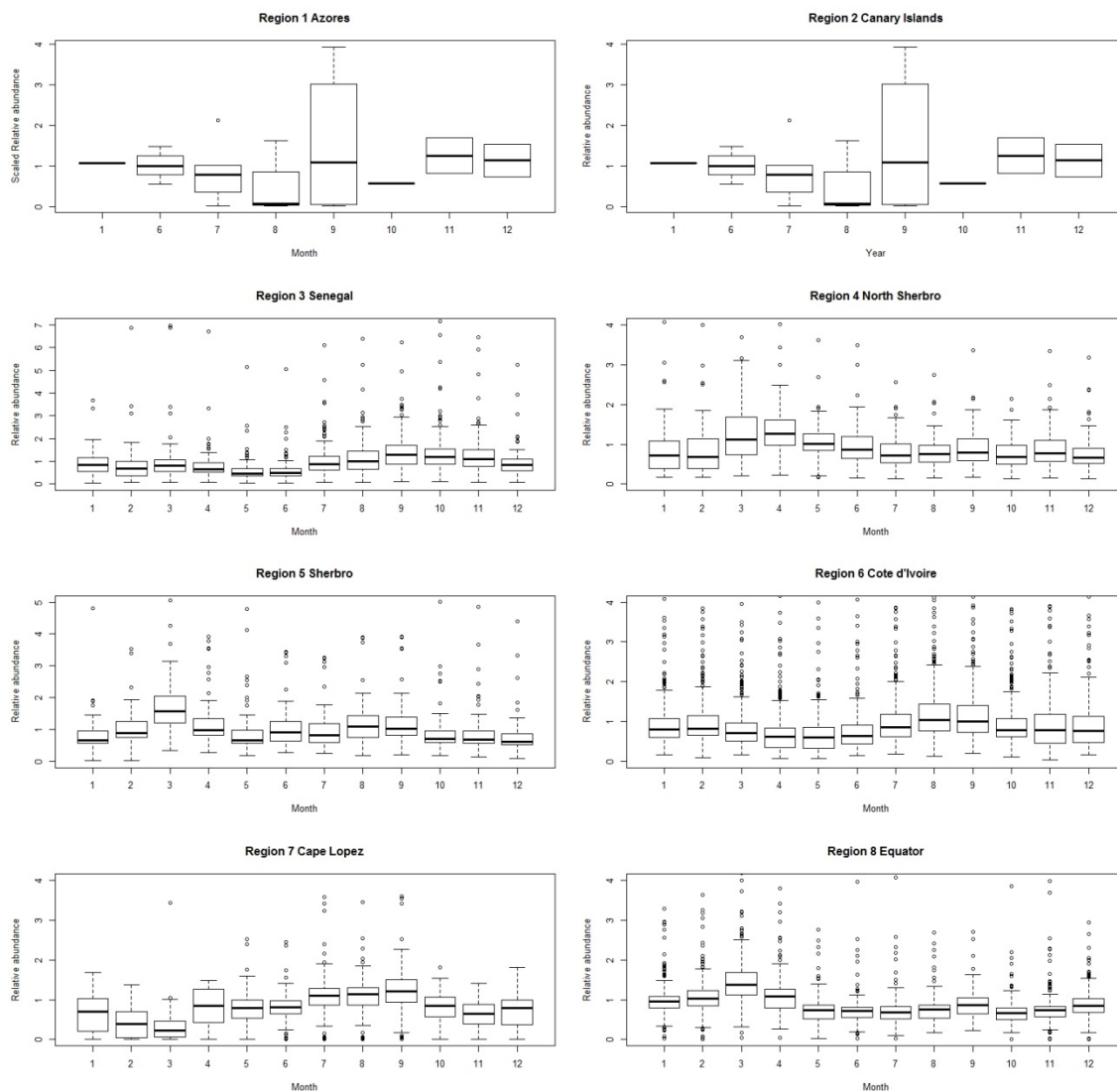


Figure A7. Standardized monthly CPUEs for yellowfin tuna.

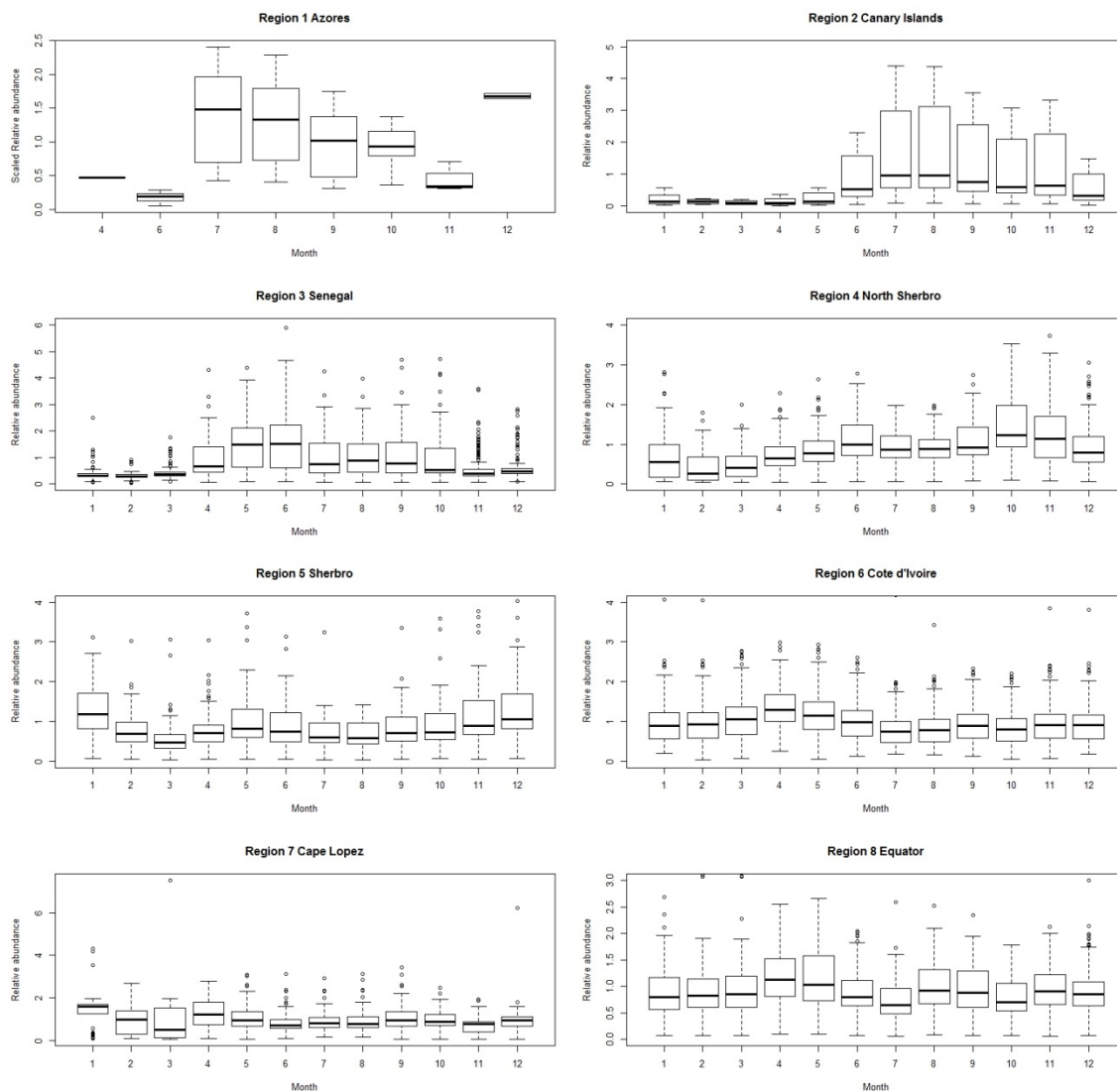


Figure A8. Standardized monthly CPUEs for skipjack tuna.

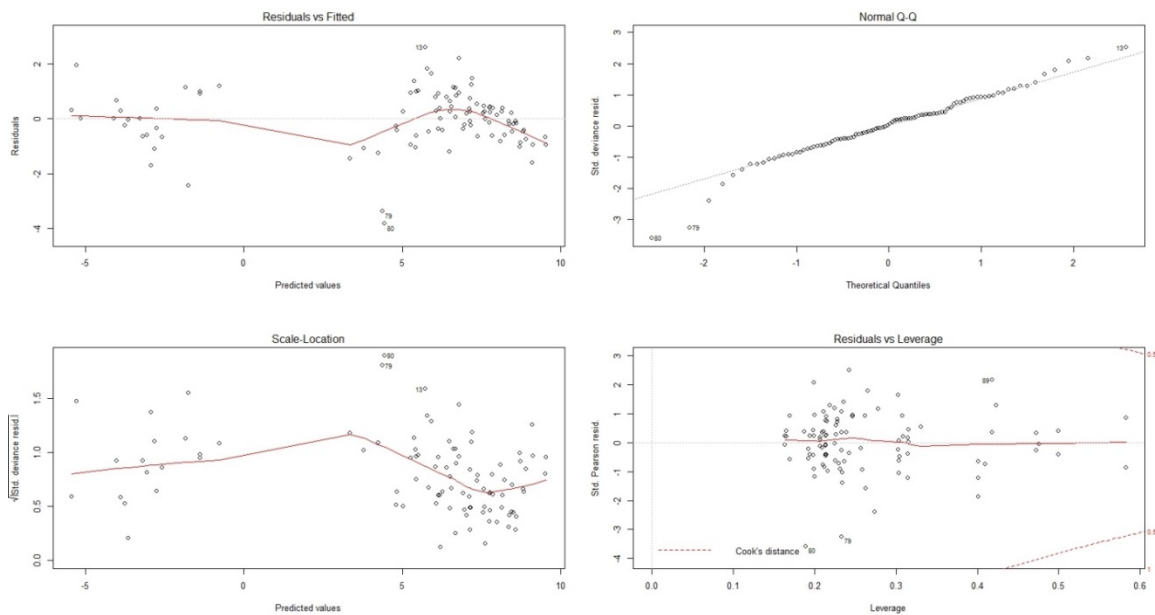


Figure A9. Region 1 – Azores GLM diagnostic plots

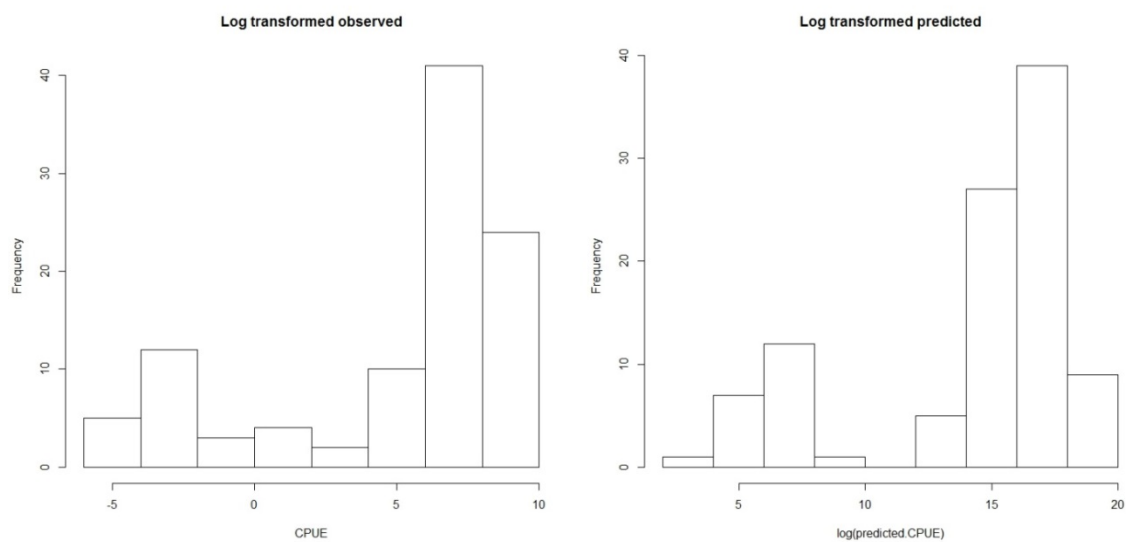


Figure A10. Region 1 – Azores Histograms of Fitted and Observed log transformed CPUE.

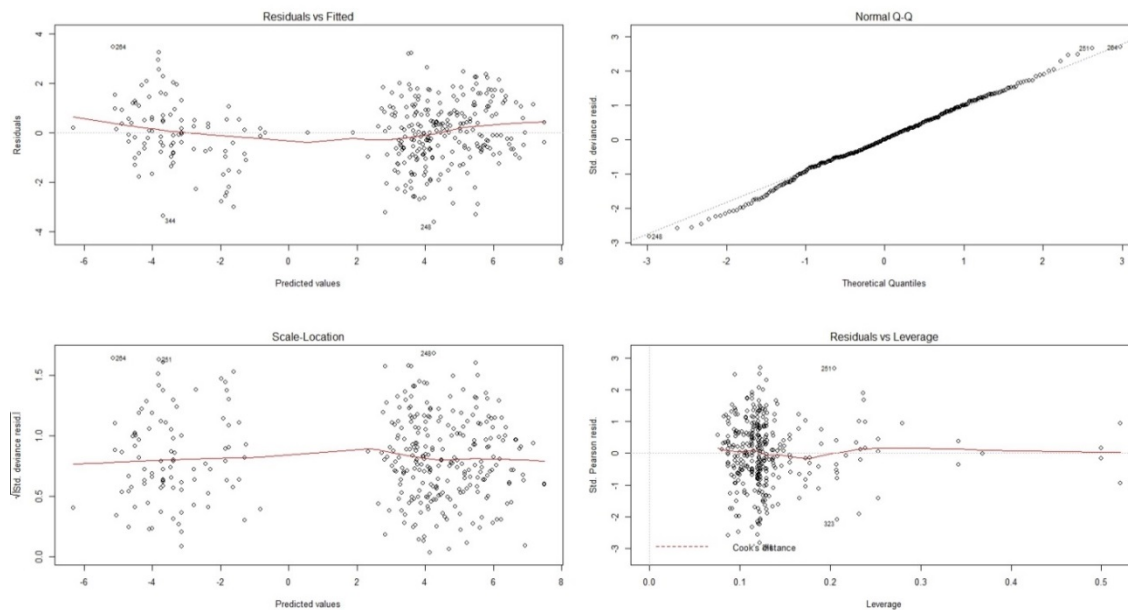


Figure A11. Region 2 – Canary Islands GLM diagnostic plots

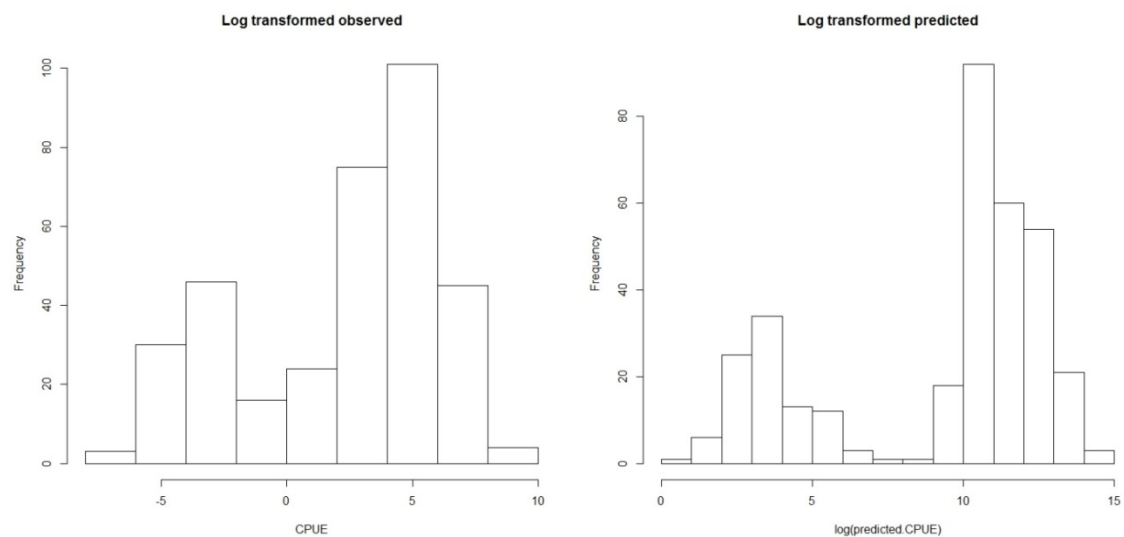


Figure A12. Region 2 – Canary Islands Histograms of Fitted and Observed log transformed CPUE.

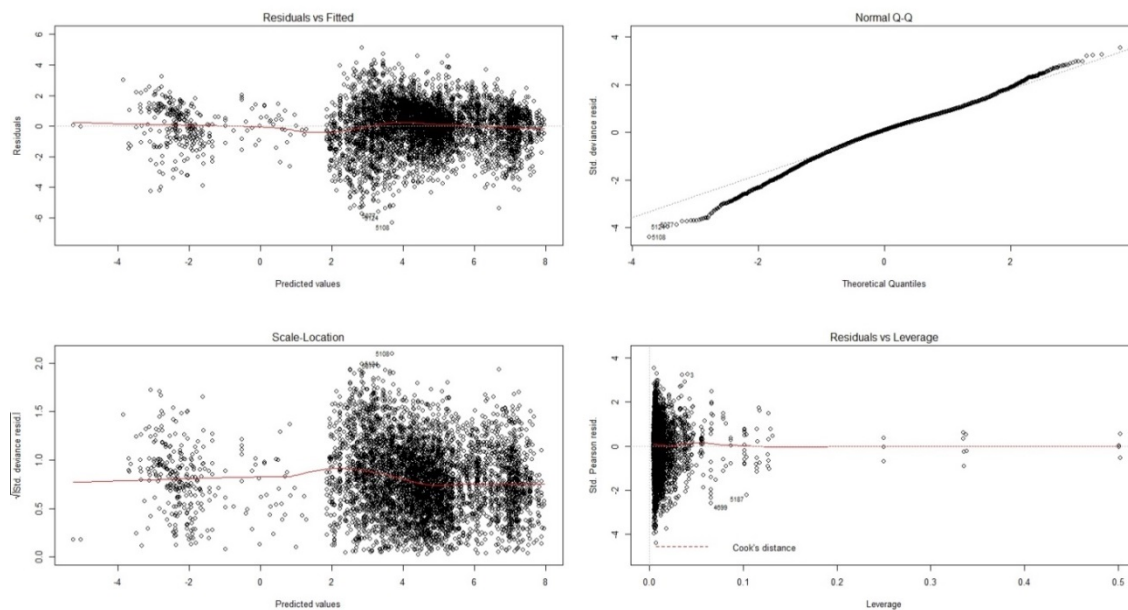


Figure A13. Region 3 – Senegal GLM diagnostic plots

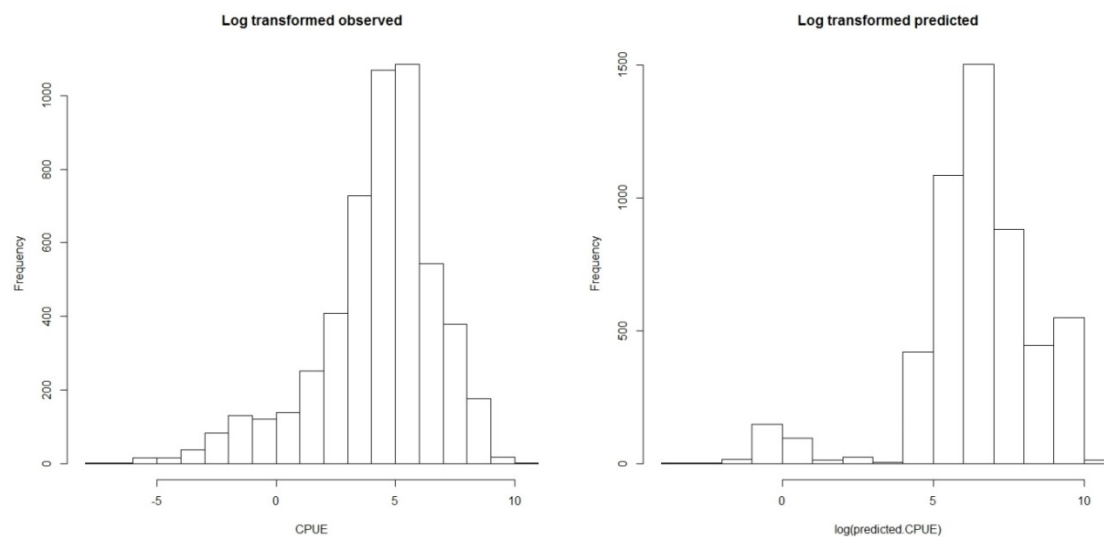


Figure A14. Region 3 – Senegal Histograms of Fitted and Observed log transformed CPUE.

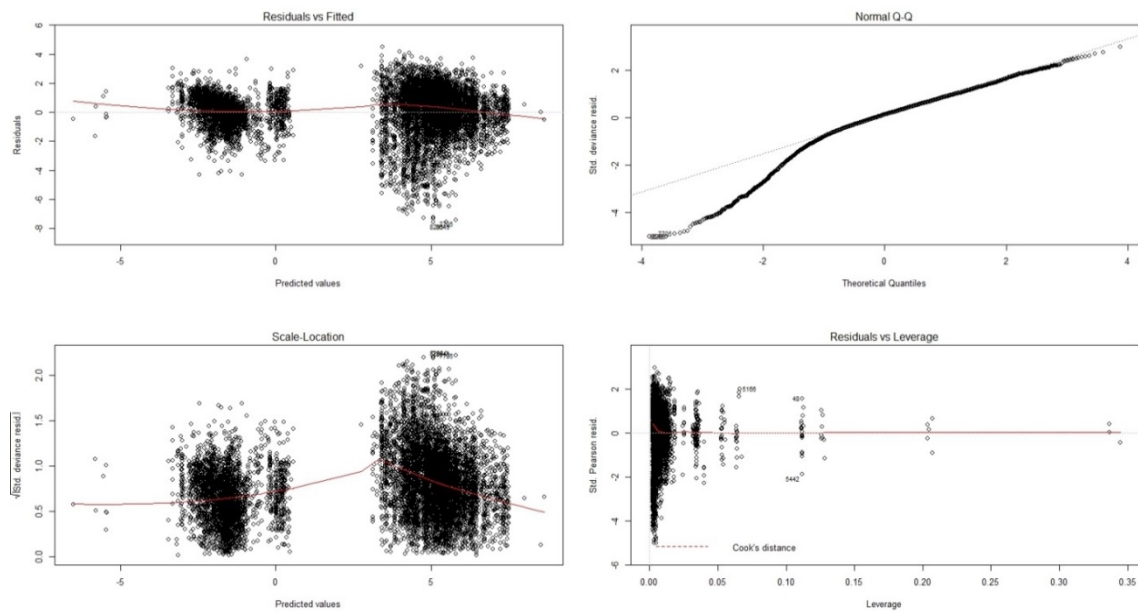


Figure A15. Region 4 – North Sherbro GLM diagnostic plots

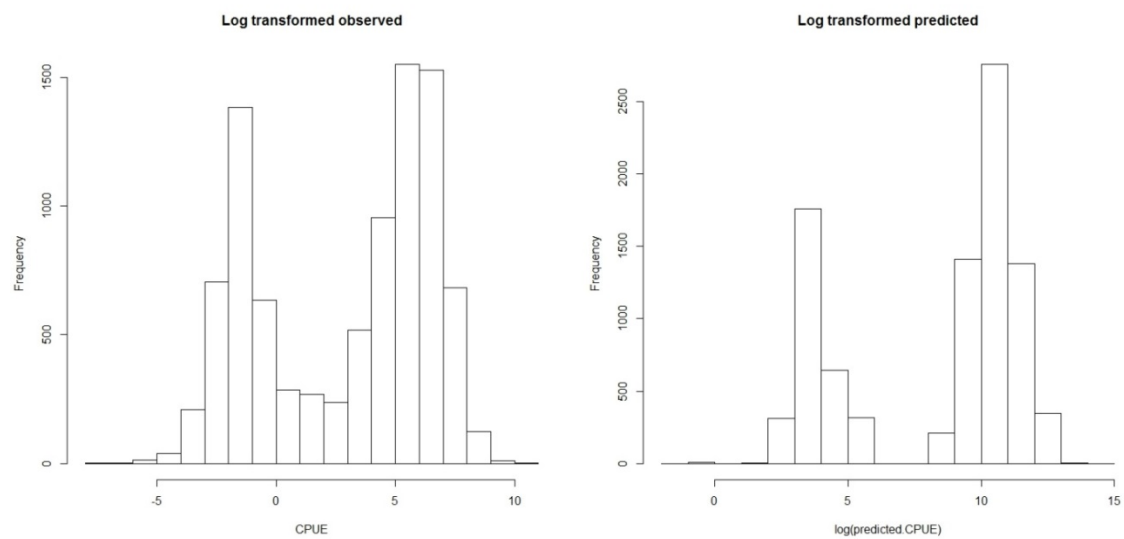


Figure A16. Region 4 – North Sherbro Histograms of Fitted and Observed log transformed CPUE.

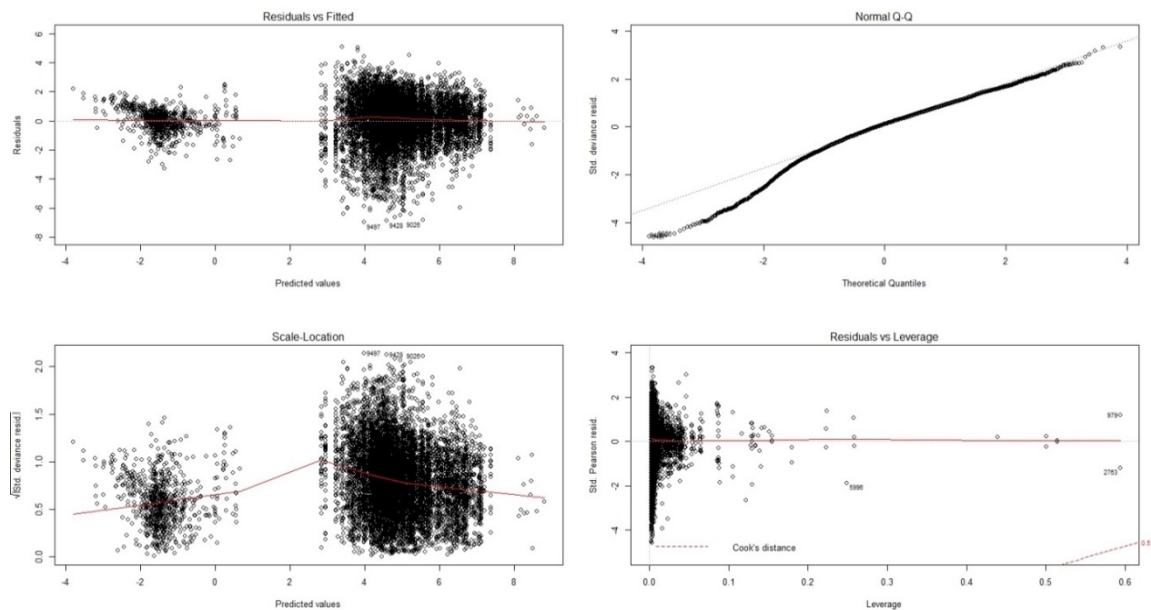


Figure A17. Region 5 - Sherbro GLM diagnostic plots

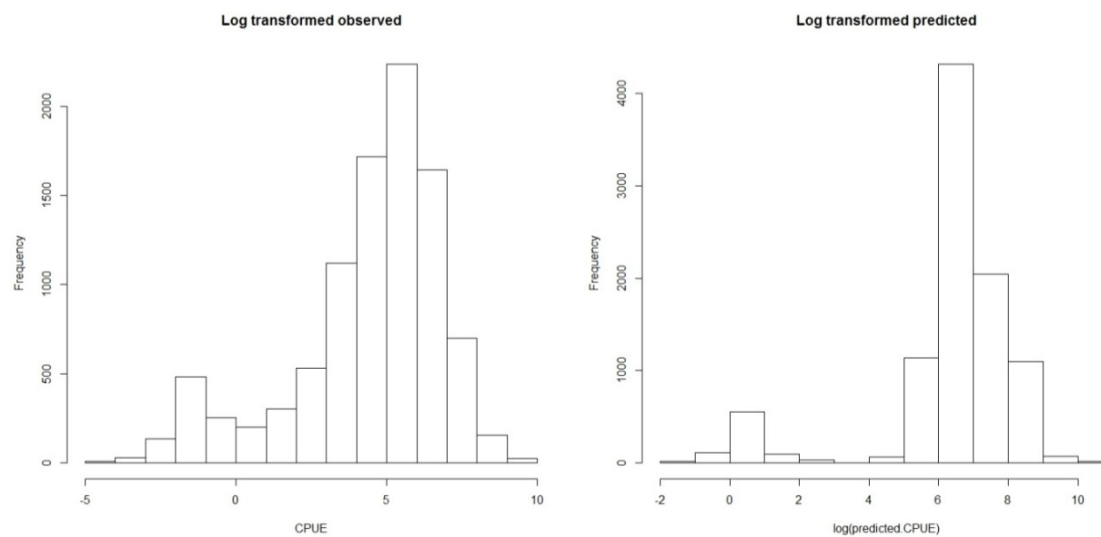


Figure A18. Region 5 - Sherbro Histograms of Fitted and Observed log transformed CPUE.

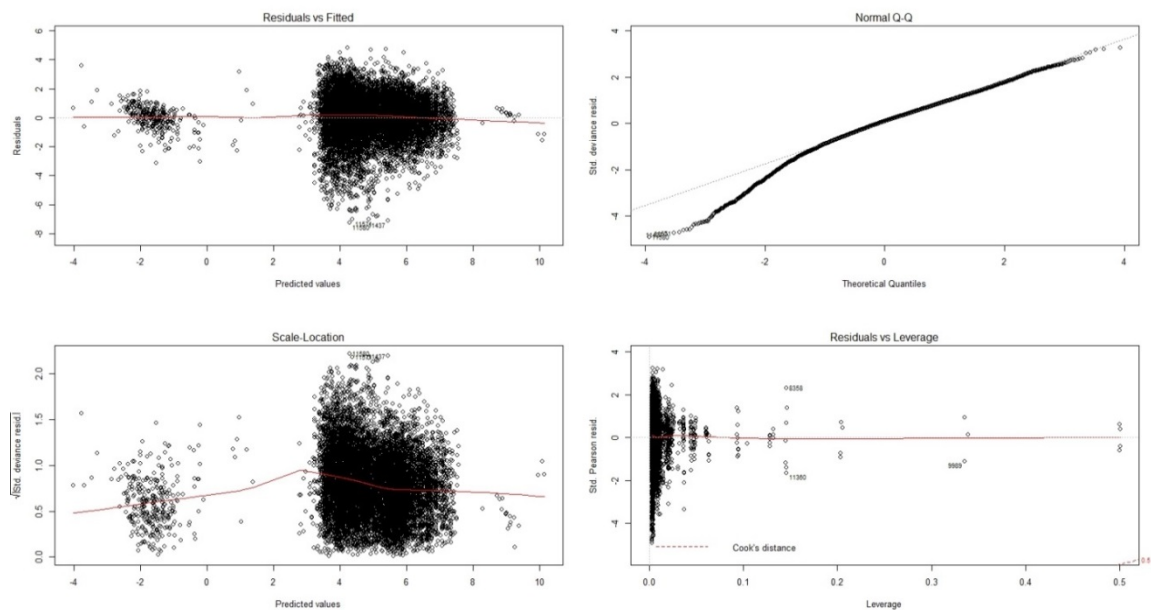


Figure A19. Region 6 – Cote d'Ivoire GLM diagnostic plots

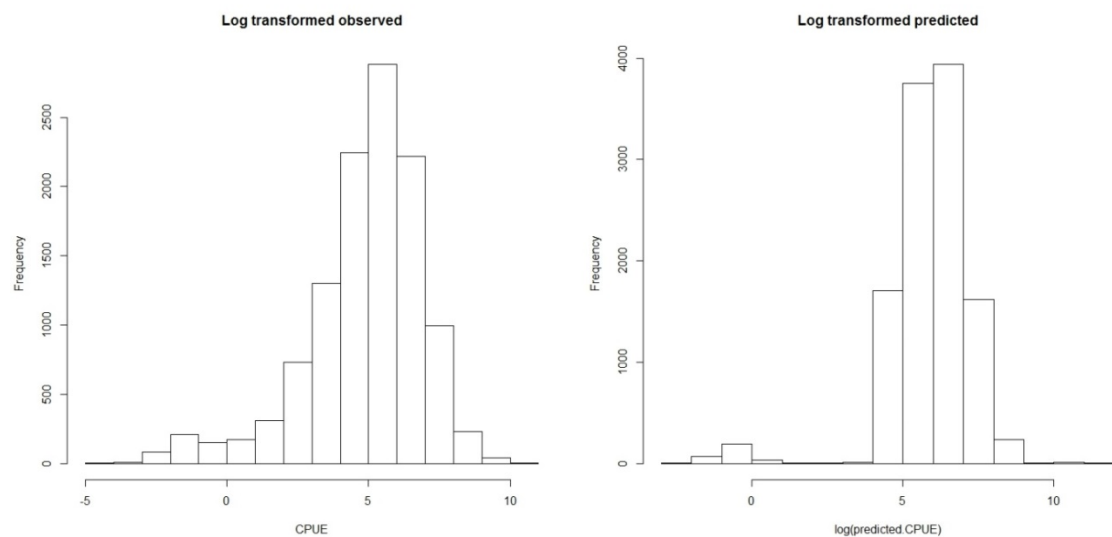


Figure A20. Region 6 – Cote d'Ivoire Histograms of Fitted and Observed log transformed CPUE.

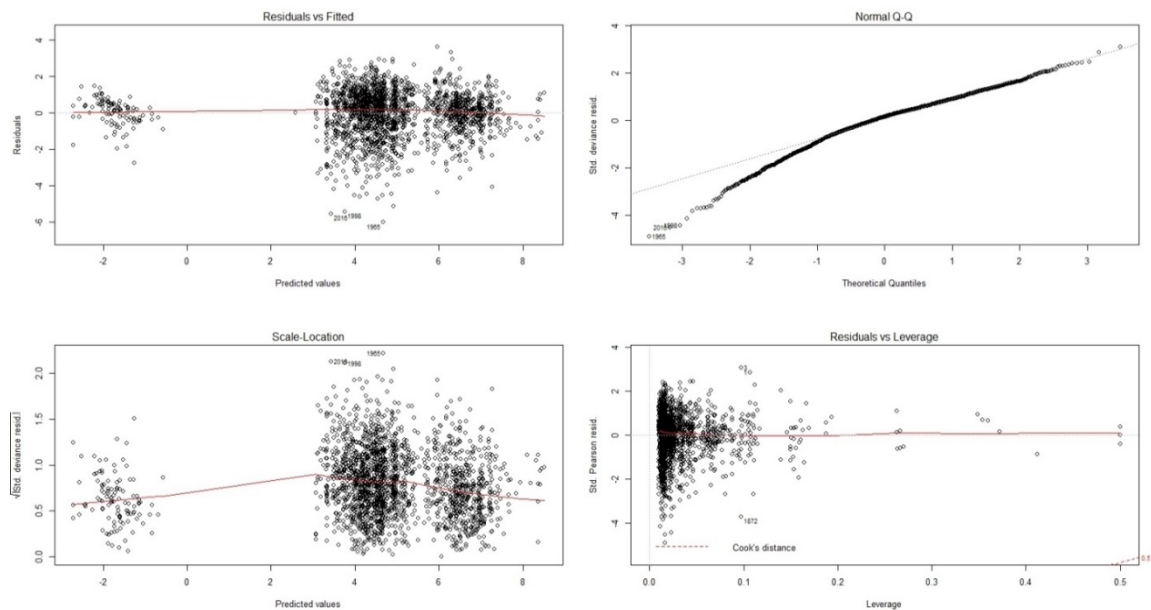


Figure A21. Region 7 – Cape Lopez GLM diagnostic plots

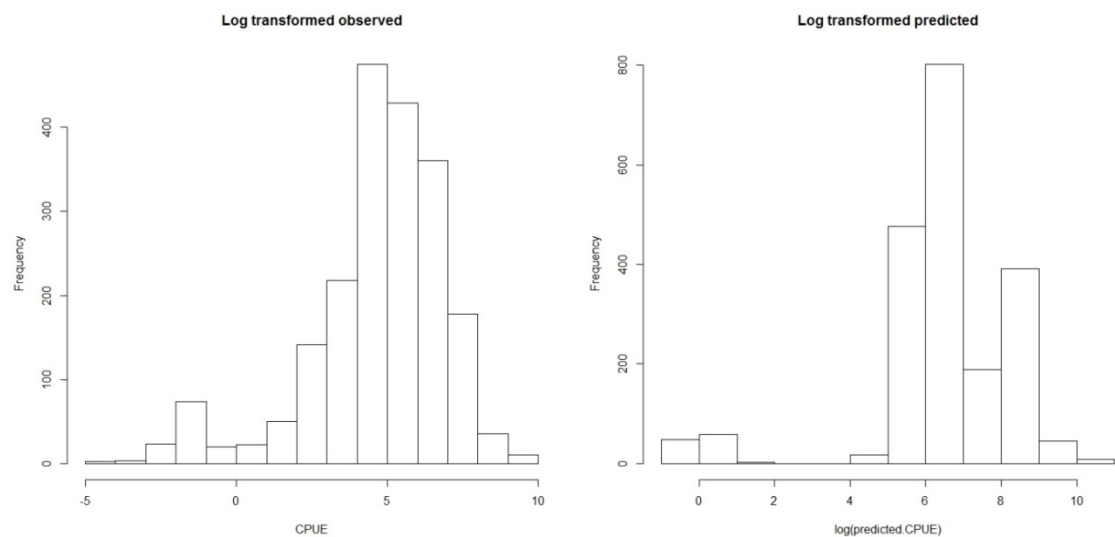


Figure A22. Region 7 – Cape Lopez Histograms of Fitted and Observed log transformed CPUE.

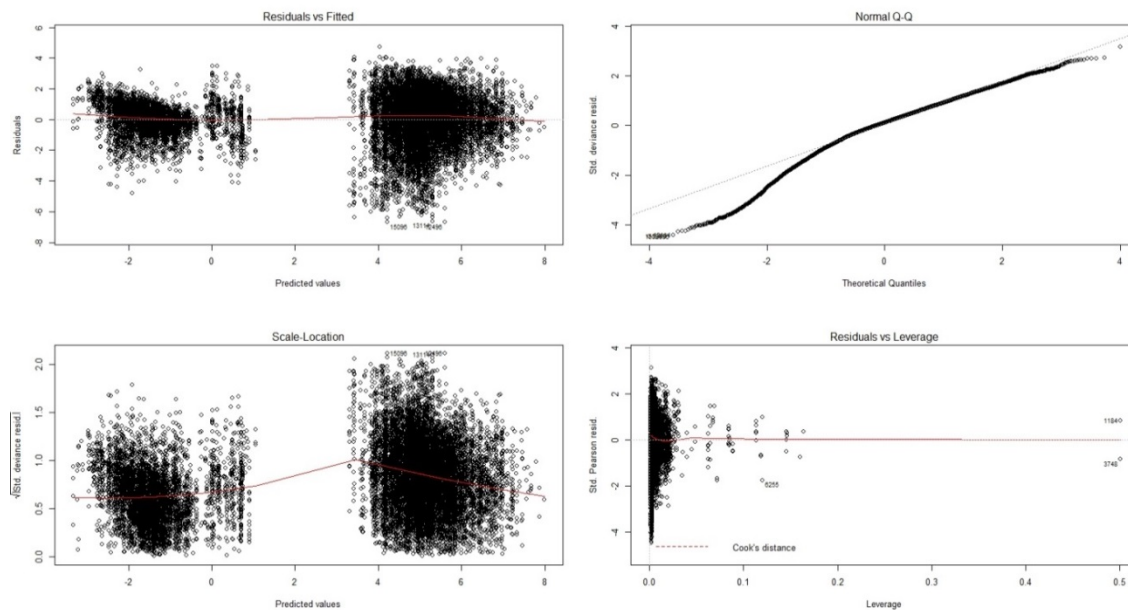


Figure A23. Region 8 – Equator GLM diagnostic plots

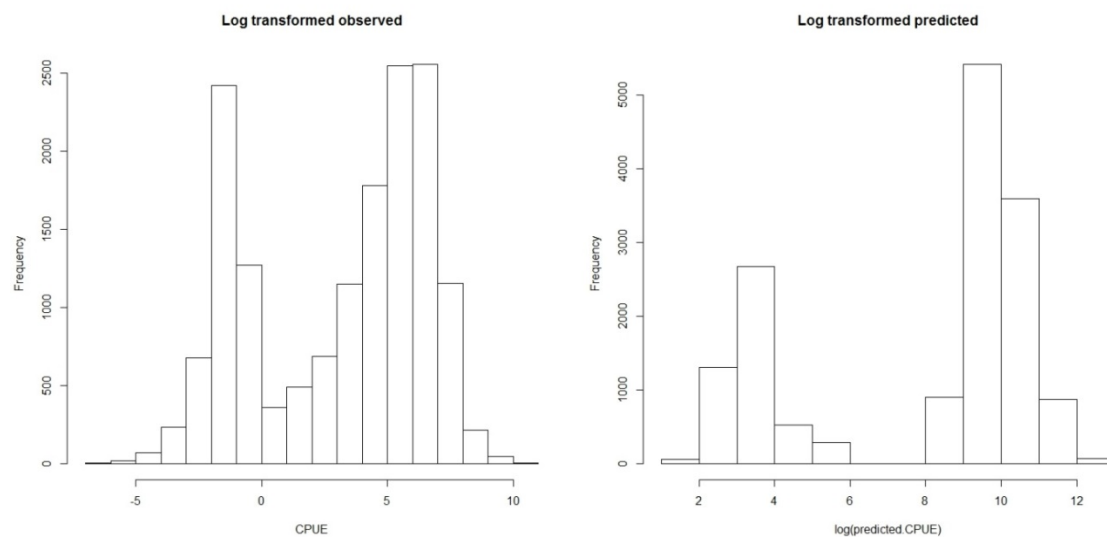


Figure A24. Region 8 - Equator Histograms of Fitted and Observed log transformed CPUE.

Skipjack tuna

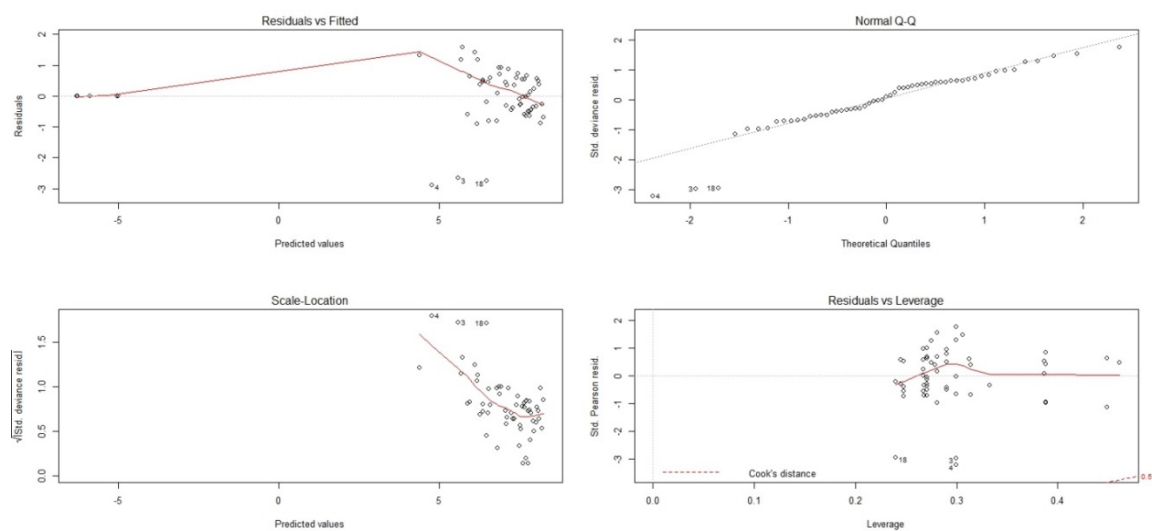


Figure A25. Region 1 – Azores GLM diagnostic plots

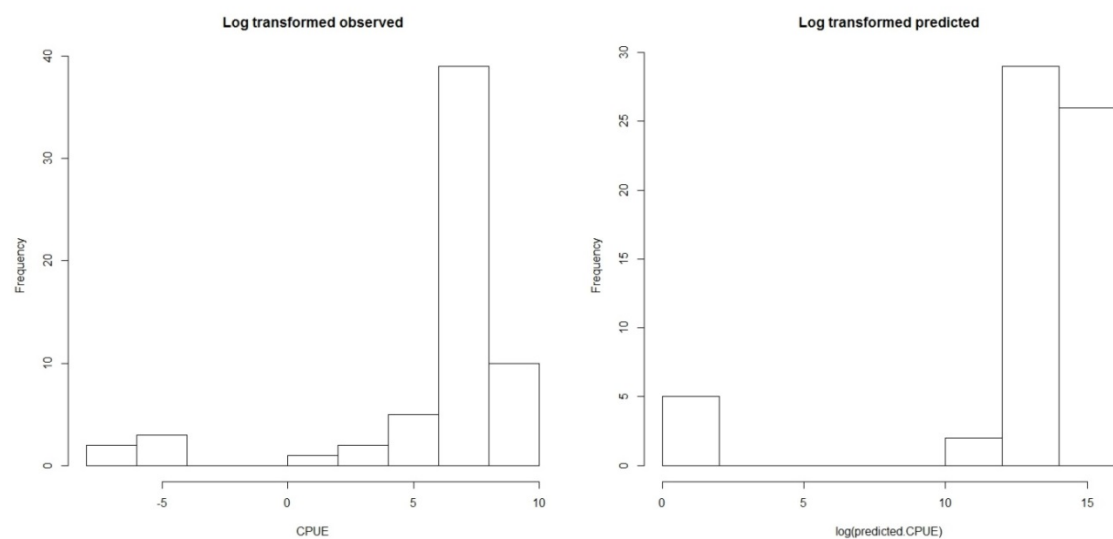


Figure A26. Region 1 – Azores Histograms of Fitted and Observed log transformed CPUE.

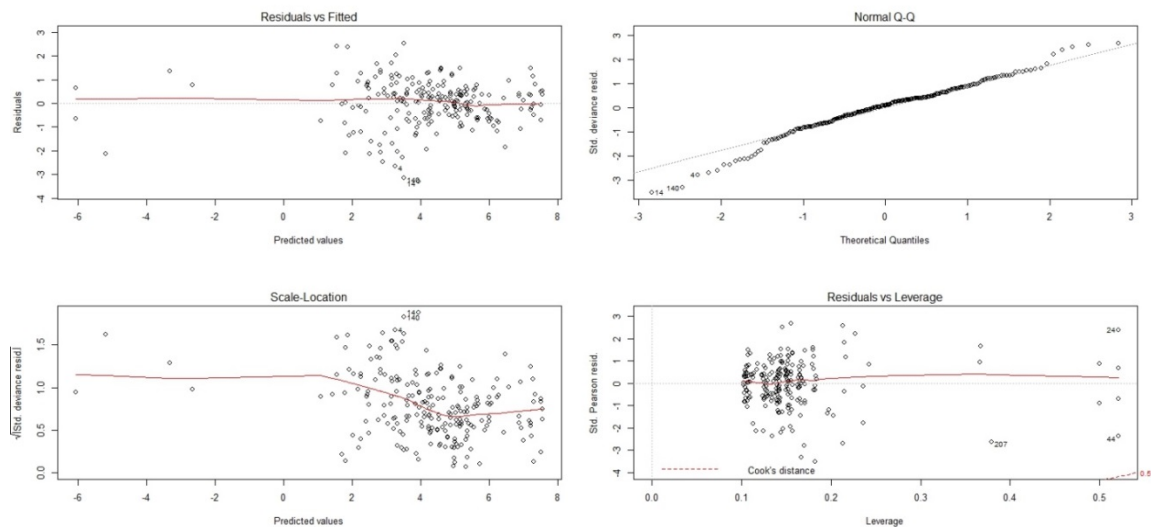


Figure A27. Region 2 – Canary Islands GLM diagnostic plots

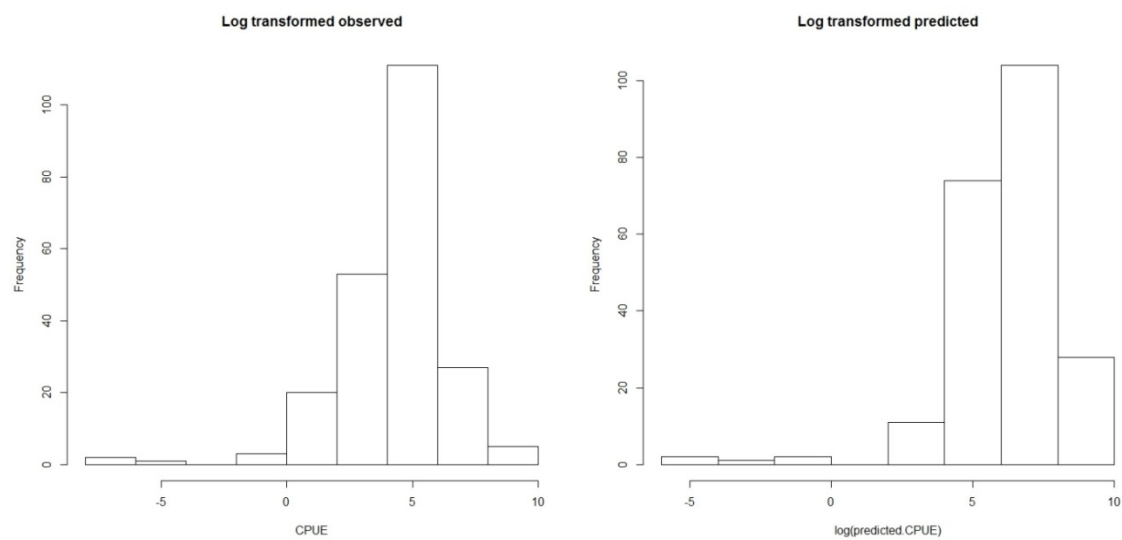


Figure A28. Region 2 – Canary Islands Histograms of Fitted and Observed log transformed CPUE.

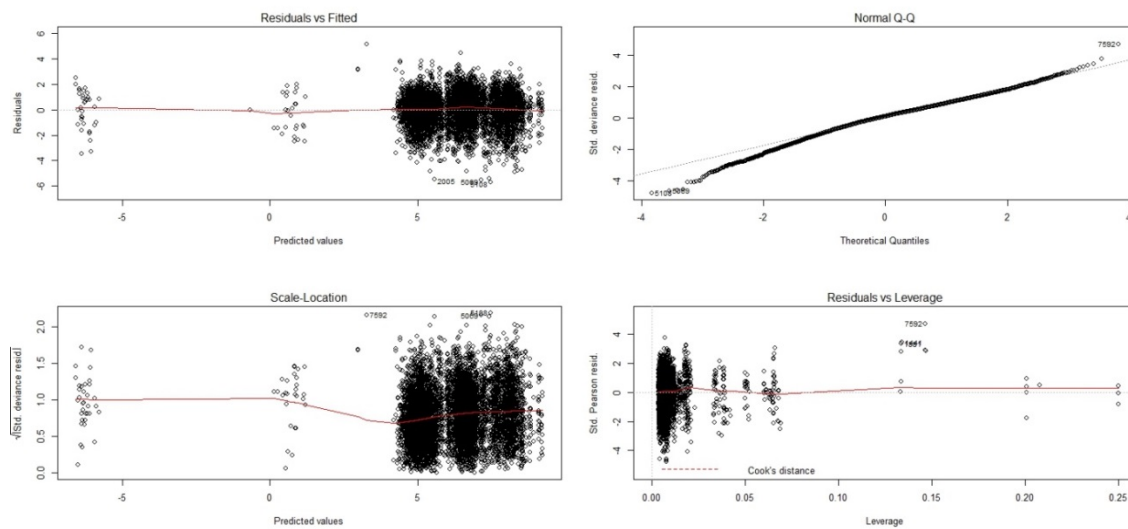


Figure A29. Region 3 – Senegal GLM diagnostic plots

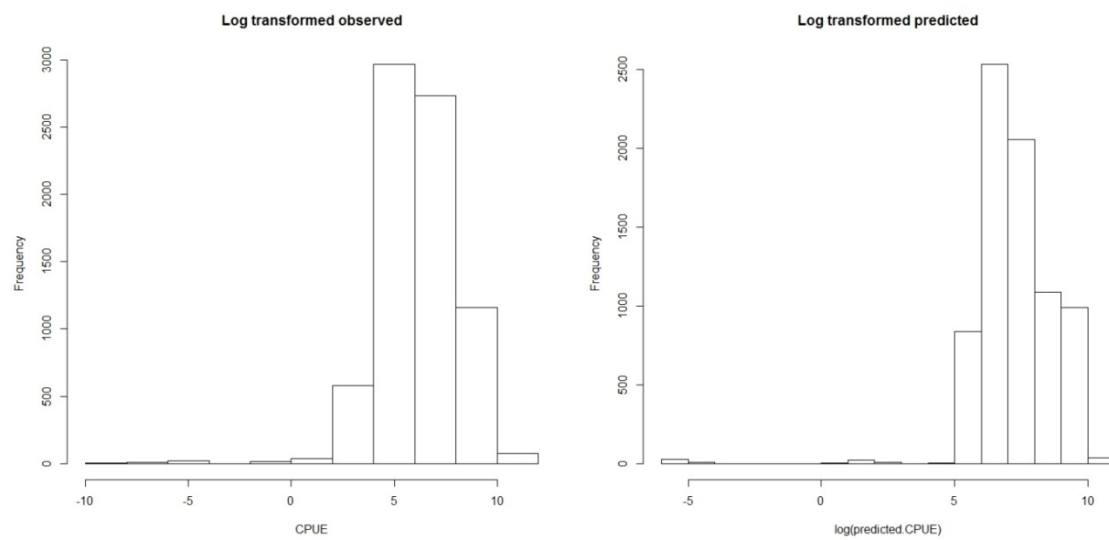


Figure A30. Region 3 – Senegal Histograms of Fitted and Observed log transformed CPUE.

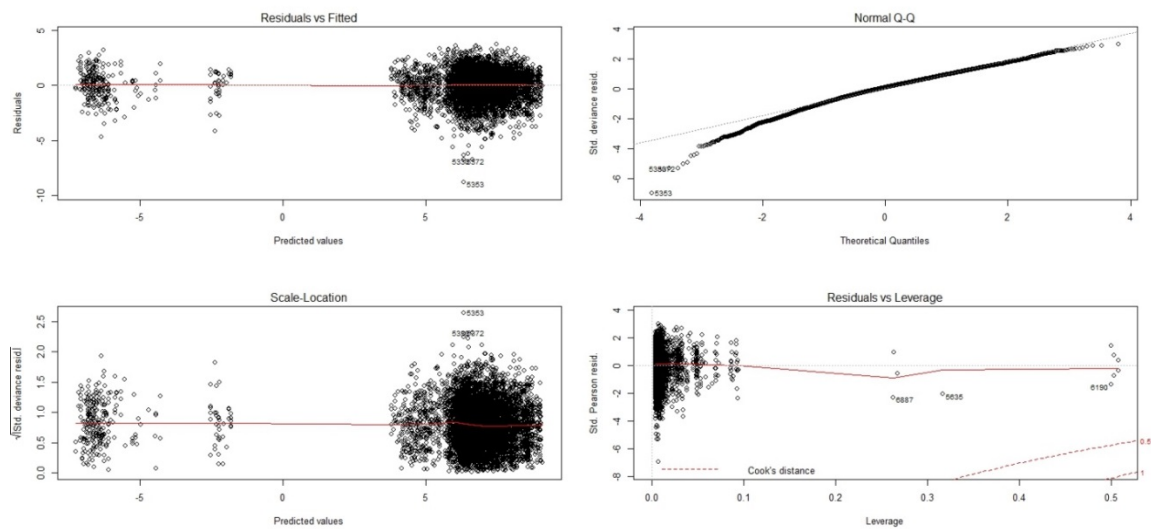


Figure A31. Region 4 – North Sherbro GLM diagnostic plots

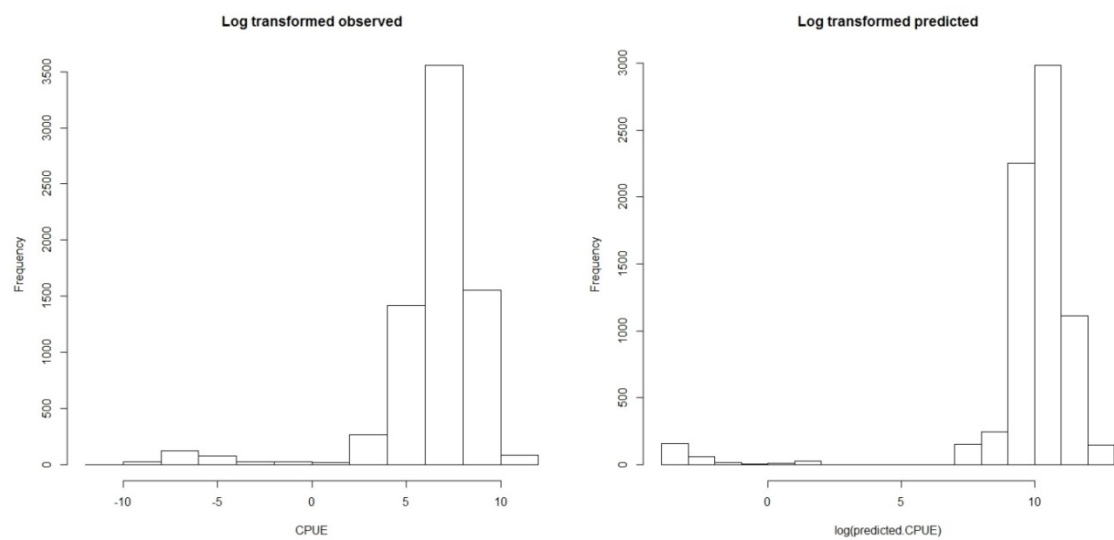


Figure A32. Region 4 – North Sherbro Histograms of Fitted and Observed log transformed CPUE.

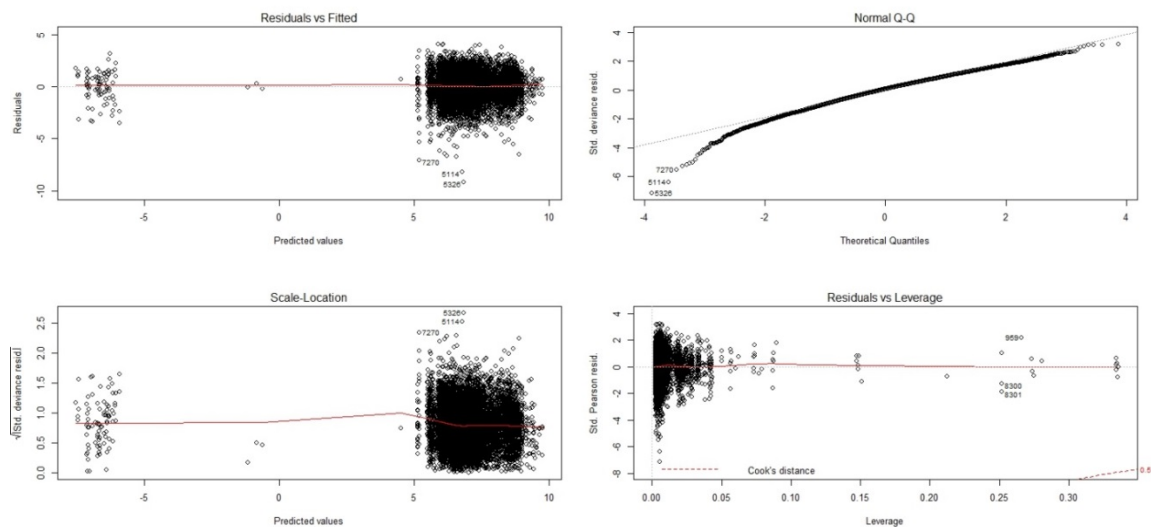


Figure A33. Region 5 - Sherbro GLM diagnostic plots

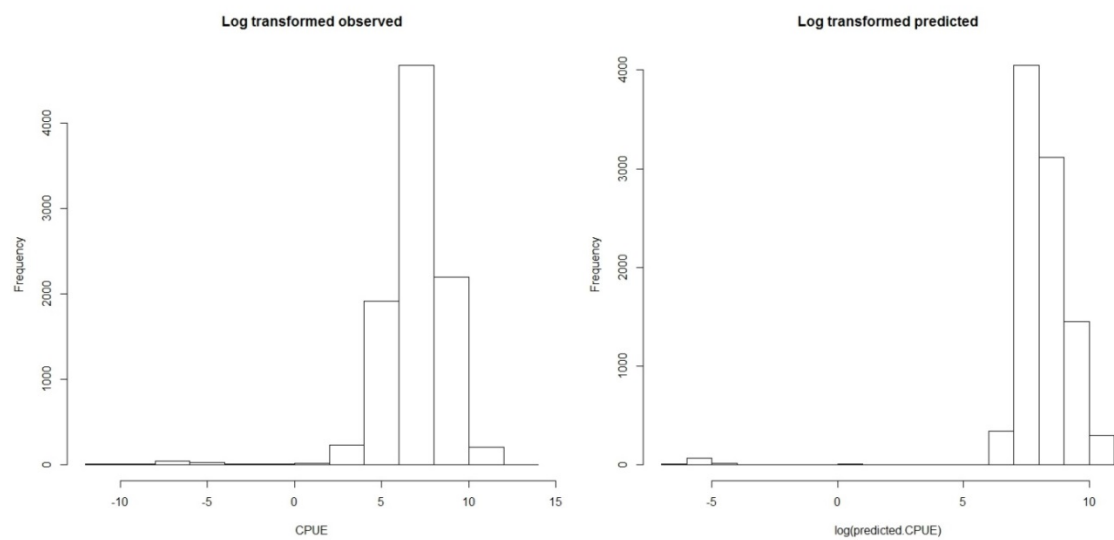


Figure A34. Region 5 - Sherbro Histograms of Fitted and Observed log transformed CPUE.

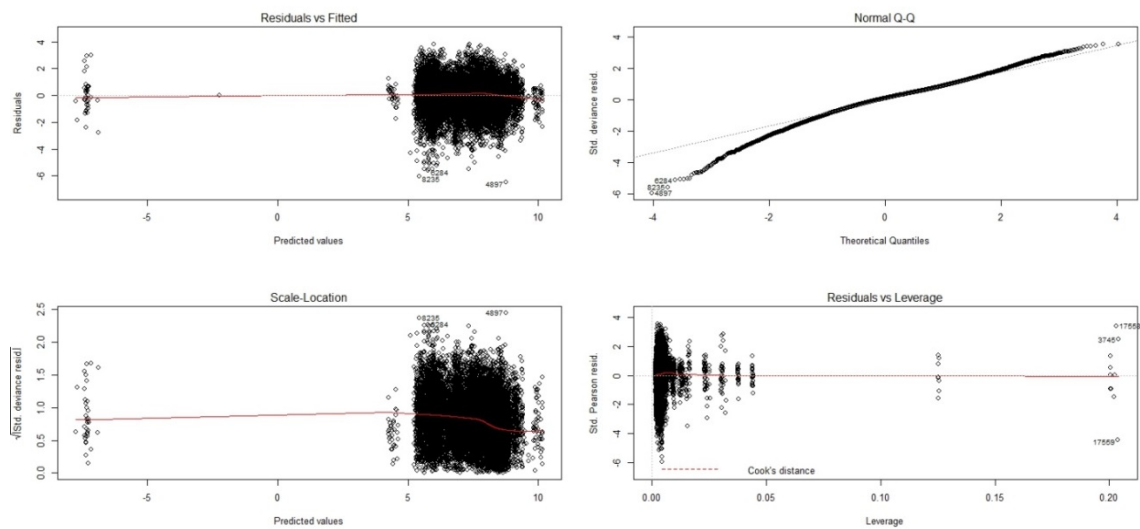


Figure A35. Region 6 – Cote d'Ivoire GLM diagnostic plots

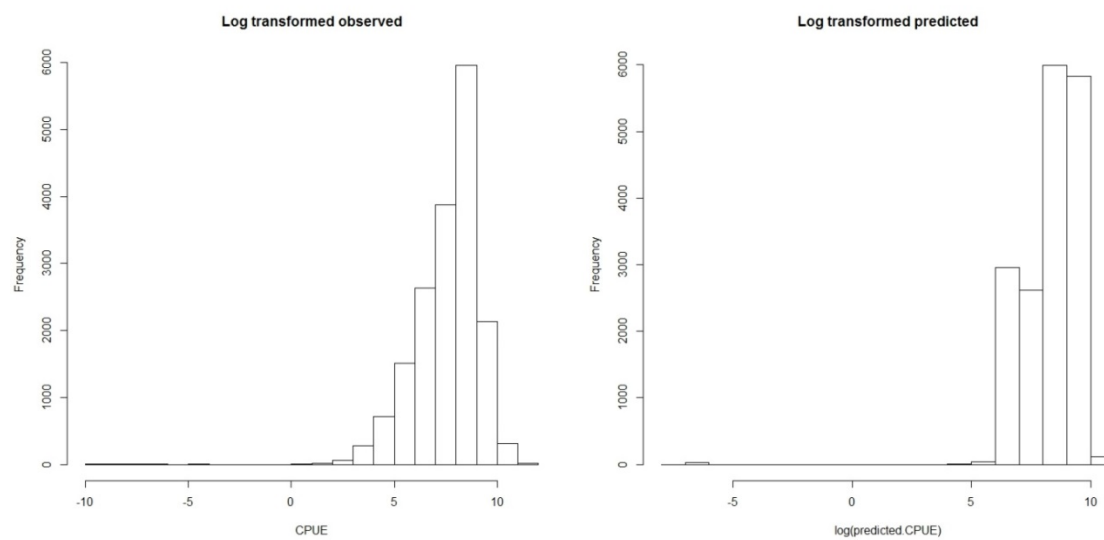


Figure A36. Region 6 – Cote d'Ivoire Histograms of Fitted and Observed log transformed CPUE.

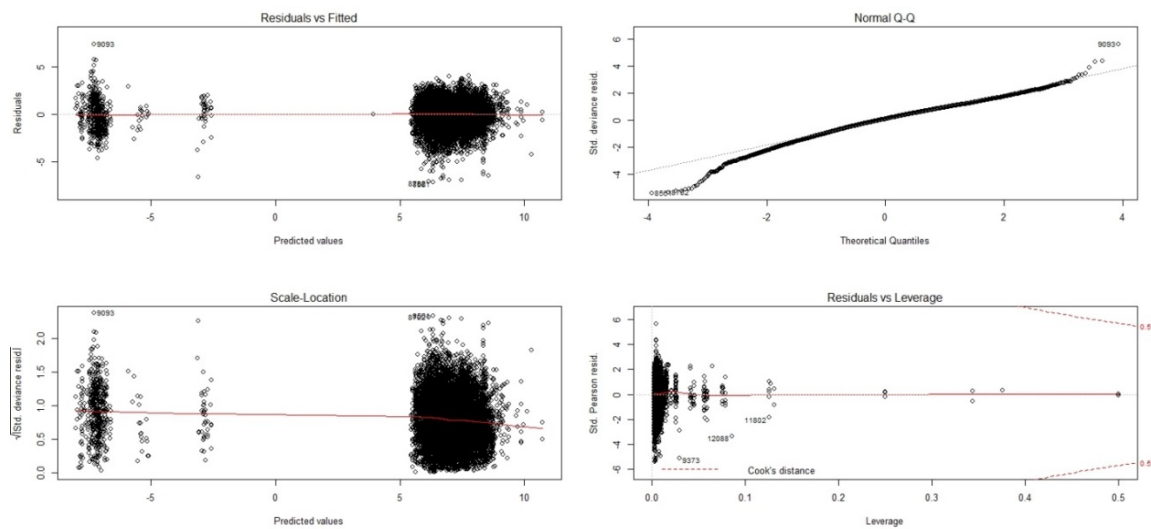


Figure A39. Region 8 – Equator GLM diagnostic plots

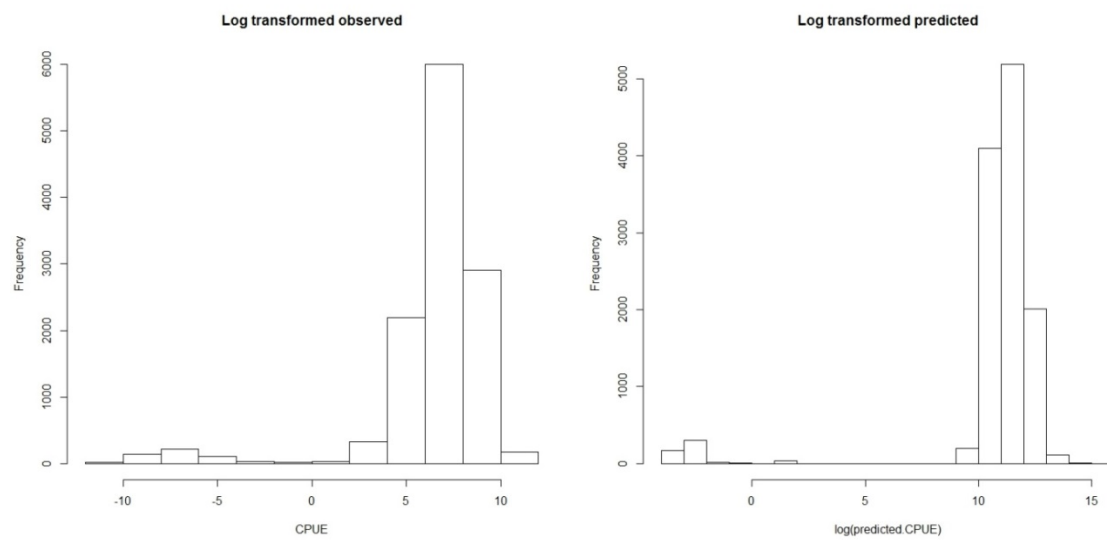


Figure A40. Region 8 - Equator Histograms of Fitted and Observed log transformed CPUE.

Yellowfin tuna

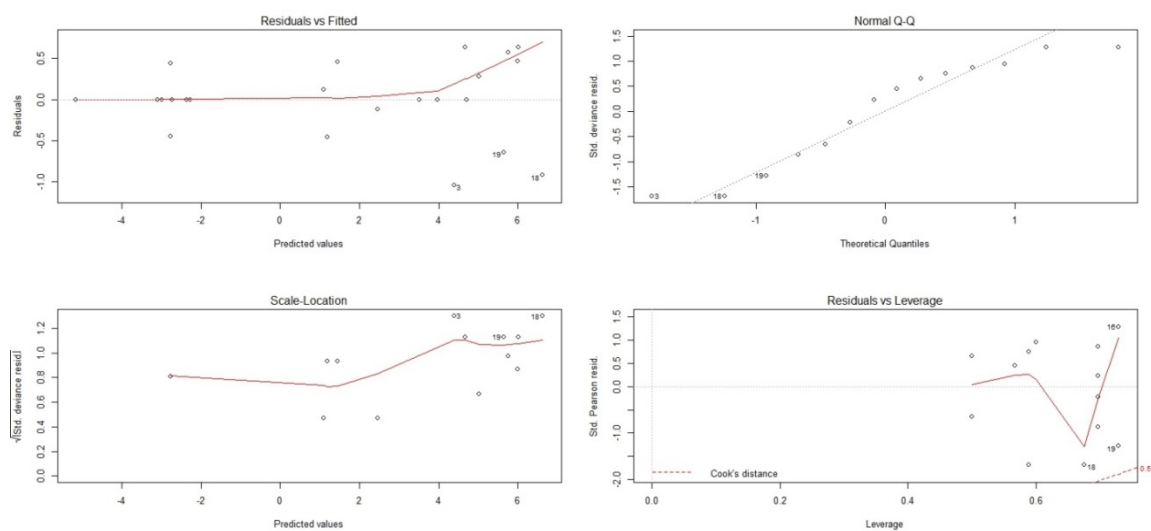


Figure A41. Region 1 – Azores GLM diagnostic plots

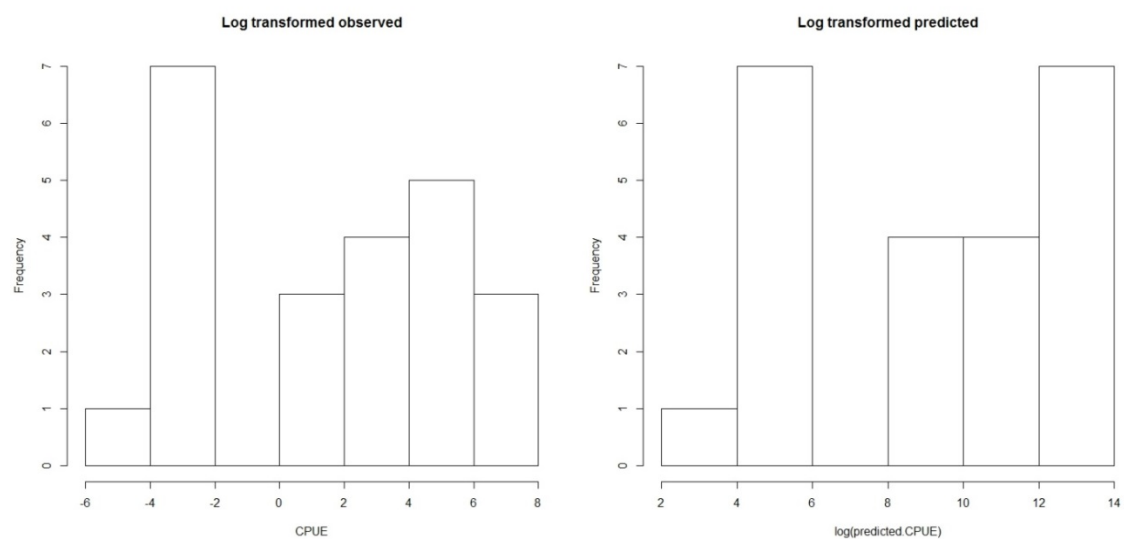


Figure A42. Region 1 – Azores Histograms of Fitted and Observed log transformed CPUE.

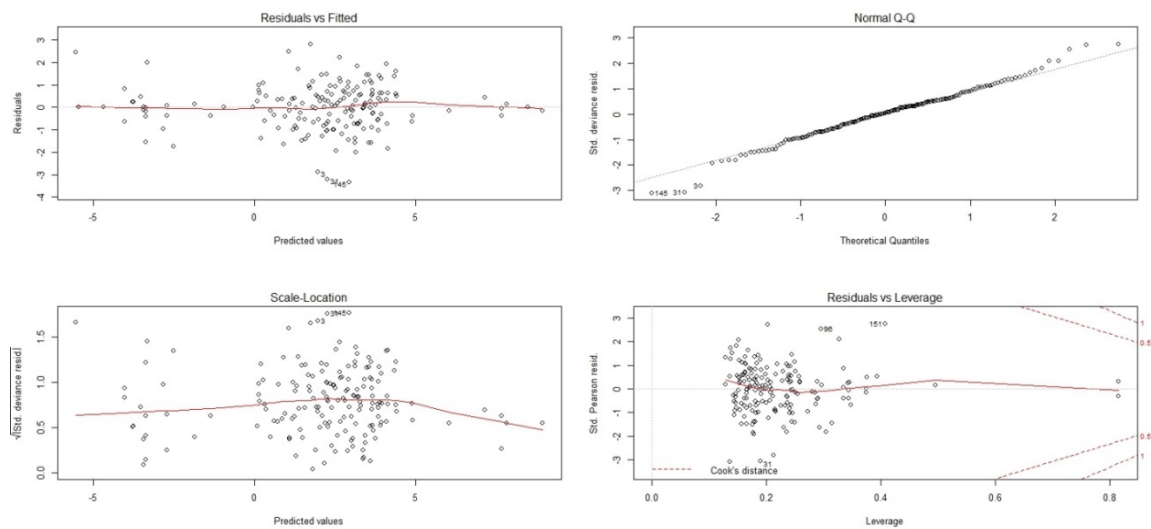


Figure A43. Region 2 – Canary Islands GLM diagnostic plots

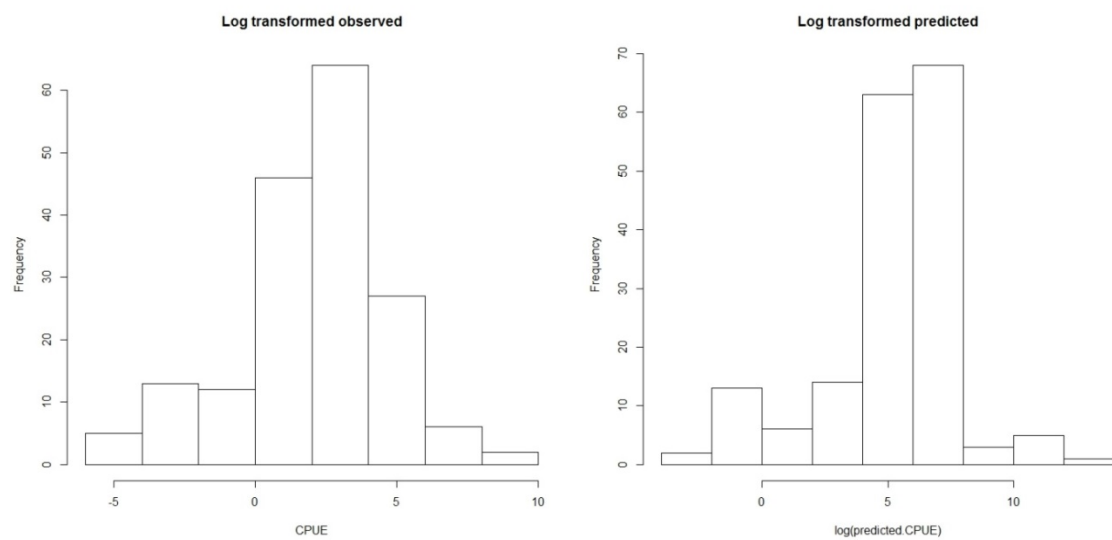


Figure A44. Region 2 – Canary Islands Histograms of Fitted and Observed log transformed CPUE.

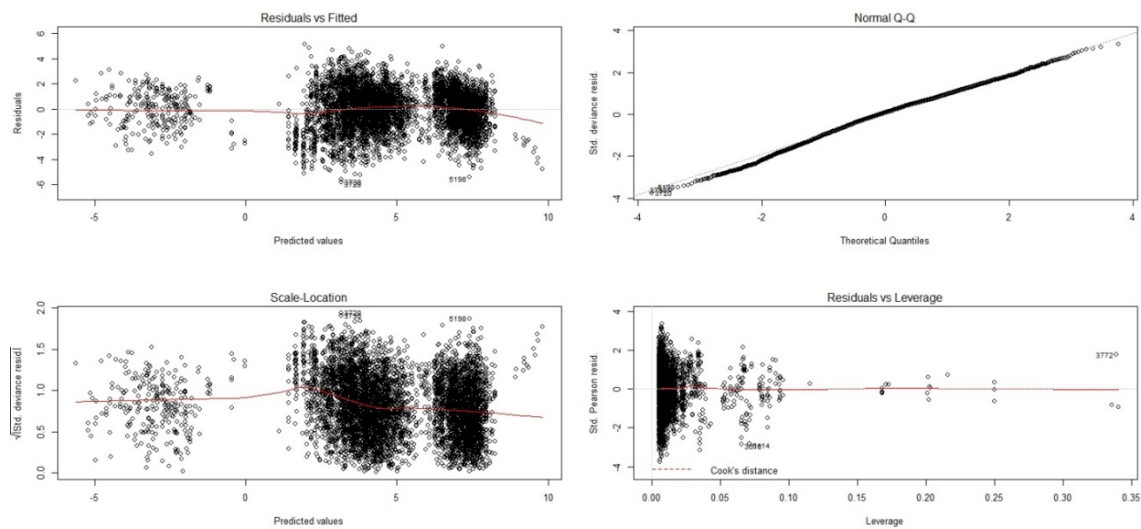


Figure A45. Region 3 – Senegal GLM diagnostic plots

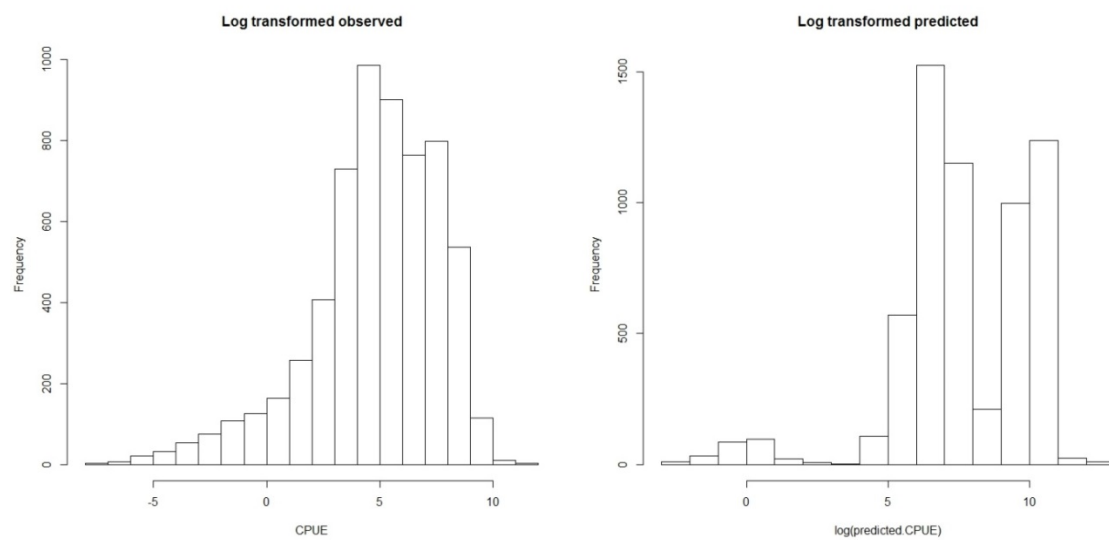


Figure A46. Region 3 – Senegal Histograms of Fitted and Observed log transformed CPUE.

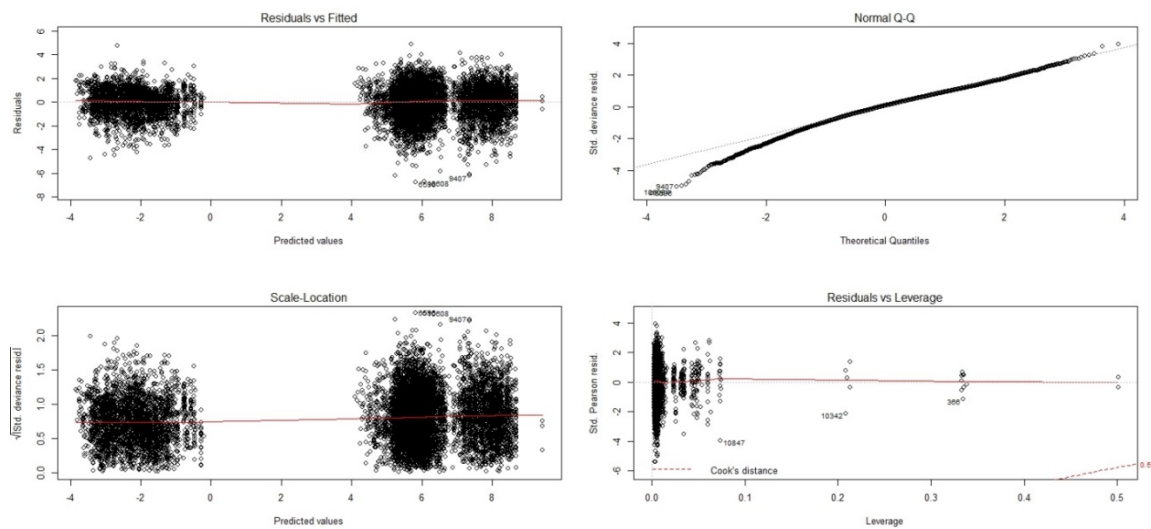


Figure A47. Region 4 – North Sherbro GLM diagnostic plots

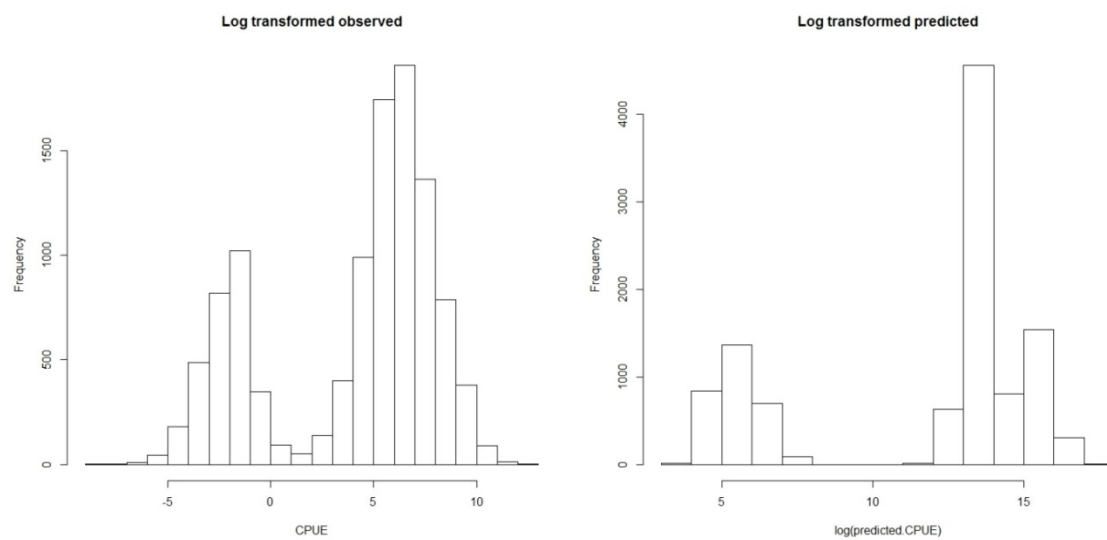


Figure A48. Region 4 – North Sherbro Histograms of Fitted and Observed log transformed CPUE

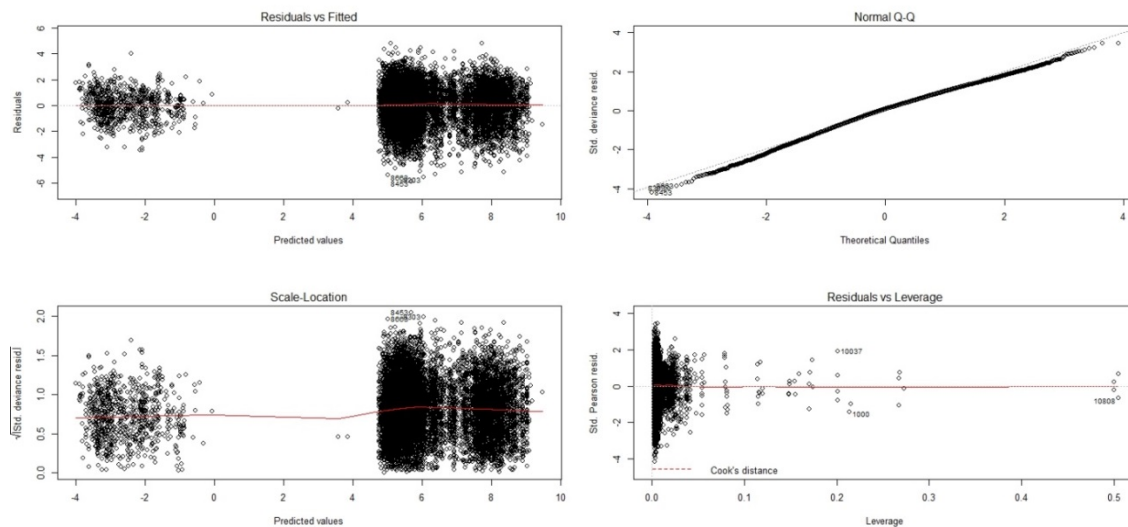


Figure A49. Region 5 - Sherbro GLM diagnostic plots

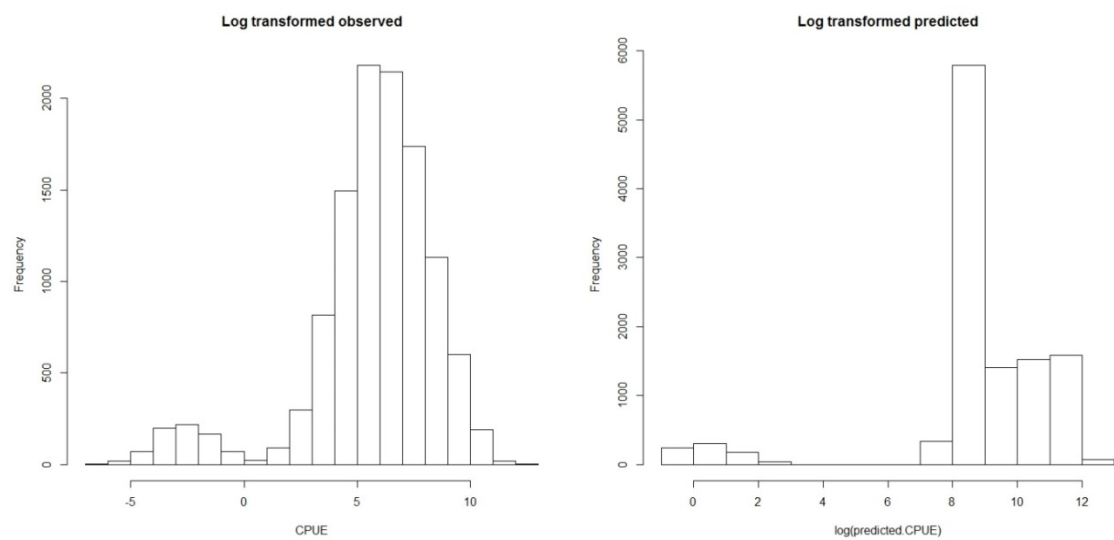


Figure A50. Region 5 - Sherbro Histograms of Fitted and Observed log transformed CPUE.

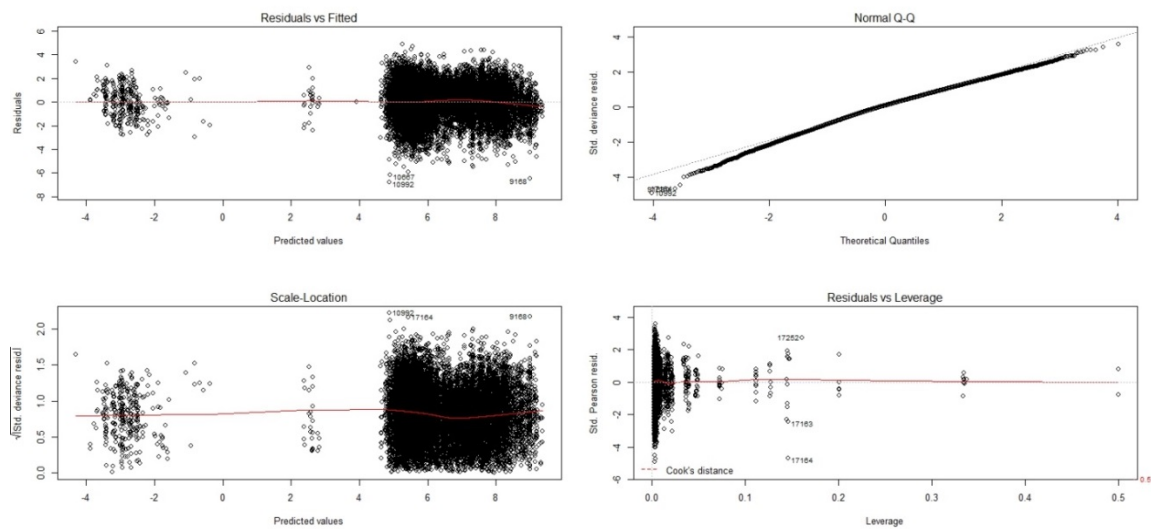


Figure A51. Region 6 – Cote d'Ivoire GLM diagnostic plots

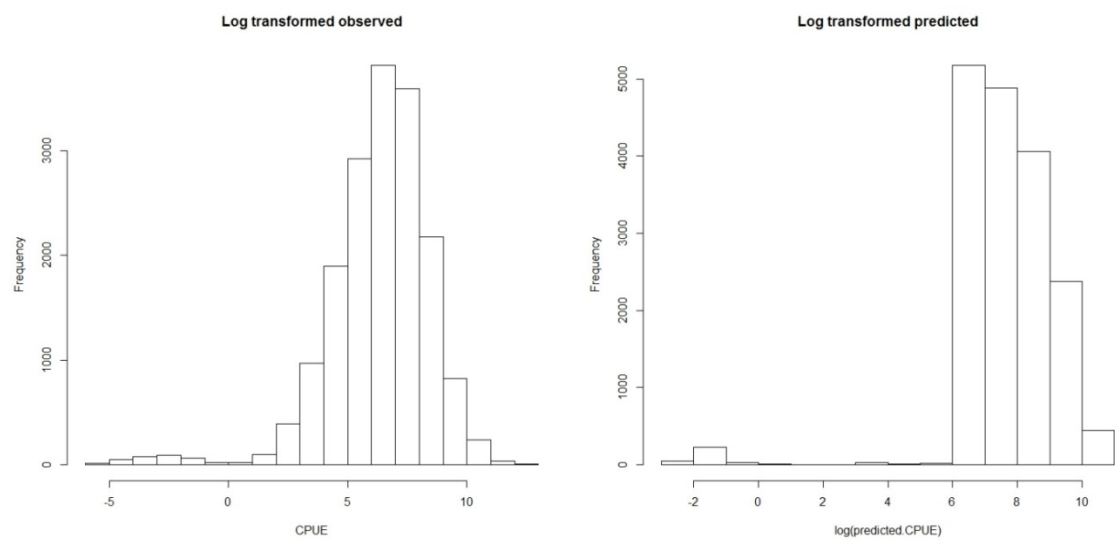


Figure A52. Region 6 – Cote d'Ivoire Histograms of Fitted and Observed log transformed CPUE

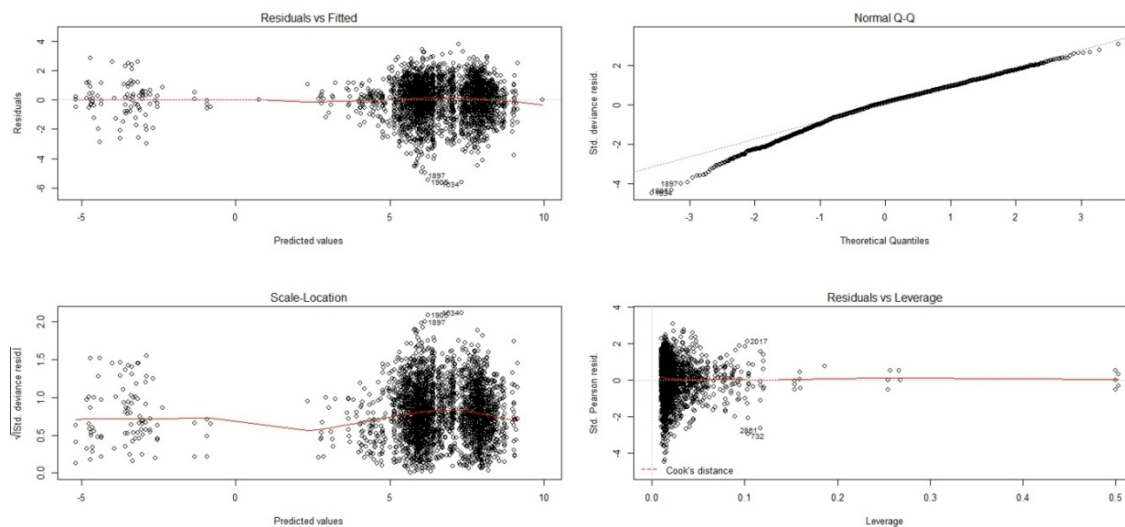


Figure A53. Region 7 – Cape Lopez GLM diagnostic plots

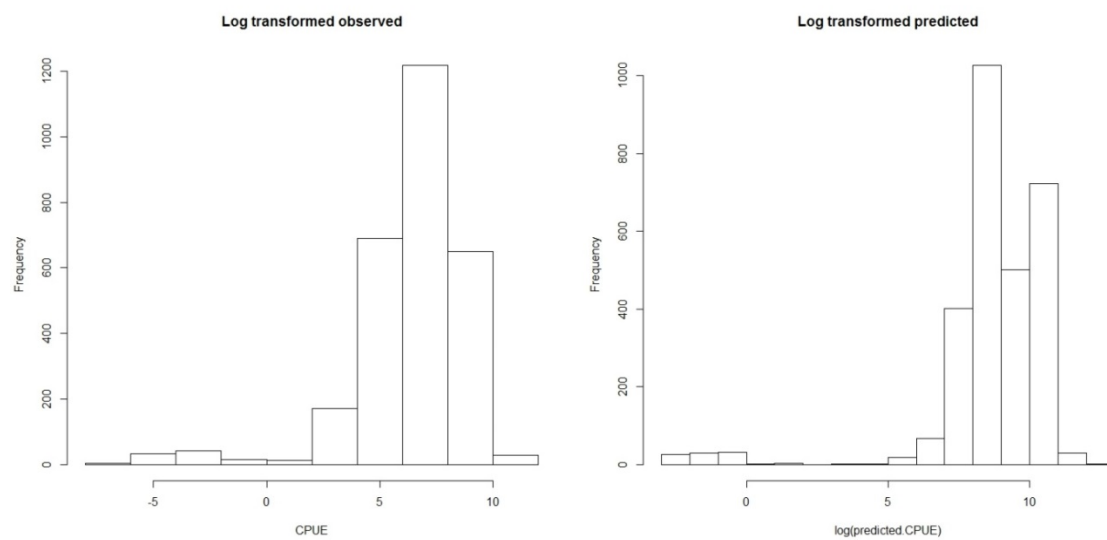


Figure A54. Region 7 – Cape Lopez Histograms of Fitted and Observed log transformed CPUE.

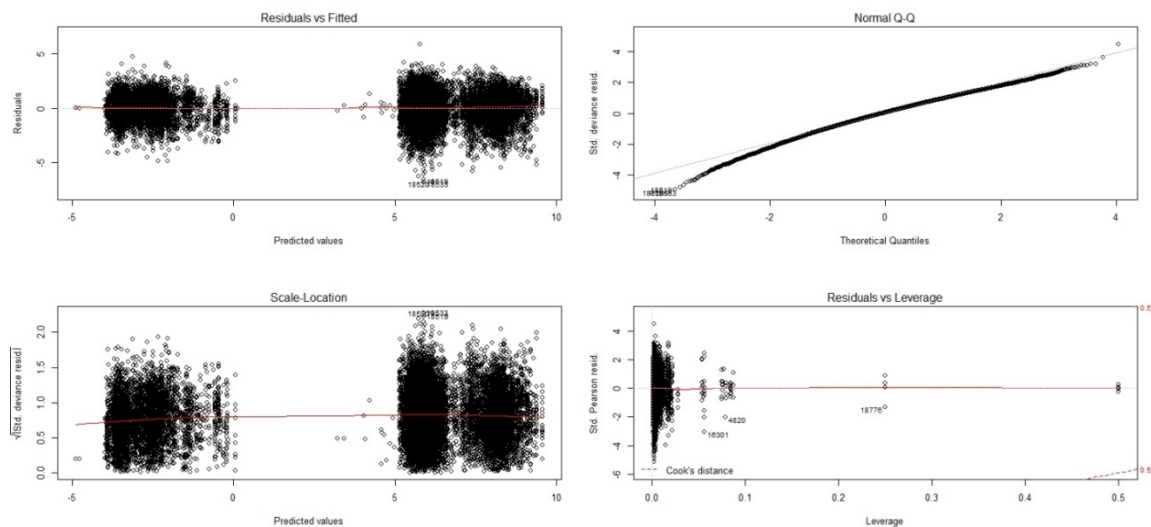


Figure A55. Region 8 – Equator GLM diagnostic plots

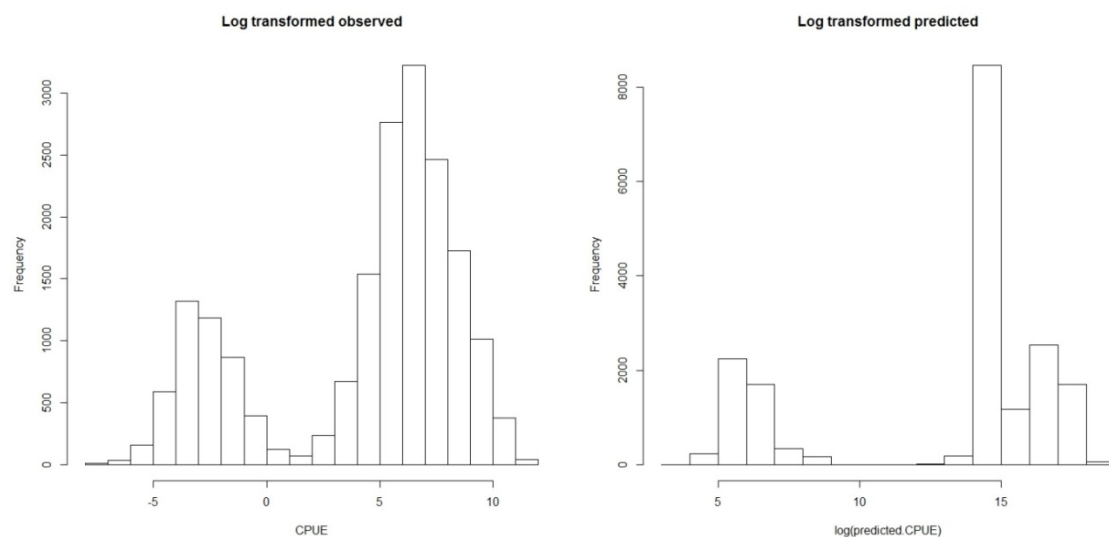


Figure A56. Region 8 - Equator Histograms of Fitted and Observed log transformed CPUE.

APPENDIX B: OPENBUGS CODE FOR THE BAYESIAN SPACE-STATE ESTIMATION MODELS DESCRIBED IN CHAPTER 3

DST Space-state model

```

model
{
  for (i in 1:arcntag){
    #calculate their survival
    for (j in 2:arclast[i]){
      #first is their first release, can be years 1 2 or 3, this is to calculate survival, second is
      first+1, last is the last year they are at large
      arcalive[i,j]~dbern(arcsurvival[i,j-1])
    }
    for(j in 1:arclast[i]){
      arcsurvival[i,j]<-exp(-(M/12))*arcalive[i,j] #if you are alive, then survival rate
      arcpcap[1,i,j] <-0 # If dead, then you are unavailable for capture
      #if you are alive, then state (movement) dependent probability of recapture
      arcpcap[2,i,j]<-arcprecovery[arcmovement[i,j],j,i]*arcreporting[arcmovement[i,j]]
      ##asuse[i,j] and apuse[i,j] tells us if the fish is alive or not (1 if alive, 2 if dead)
      arcapuse[i,j] <- arcalive[i,j] + 1
      arcreturned[i,j]~dbern(arcpcap[arcapuse[i,j],i,j])
      #write out the probabilities of being recaptured: for recovery region, year j, and
      individual i
      for (k in 1:4){
        arcprecovery[k,j,i]<-1-exp(-(F_at_age[k]/12))
      }
    }
  }
  #estimate movement rates, arcmovement is which region (1,2,3,4) the fish is in at time j
  for (j in 1:1) {
    arcmovement[i,j]~dcat(arcpsi[arcmark_region[i],1:4])
  }
  for (j in 2:arclast[i]) {
    arcmovement[i,j] ~ dcat(arcpsi[arcmovement[i,j-1],1:4]) #psi[p,s] is the probability of
    moving from region p to region
  }
}
}
}
###priors:#
for(p in 1:4){
  arcpsi[p,1:4] ~ ddirch(alpha[p,1:4])
  for (n in 1:4){
    psi[n,p]<-arcpsi[n,p]
  }
}
}
M~dunif(0,10)
for (j in 1:4){
  F_at_age[j]~dunif(0,10)
}

```

```

    }
  for (i in 1:ntags){
    #calculate their survival
    for (j in second[i]:last[i]){
      alive[i,j]~dbern(survival[i,j-1])
    }
    for(j in first[i]:last[i]){
      survival[i,j]<-exp(-M)*alive[i,j]
      pcap[1,i,j] <-0
      pcap[2,i,j]<-precovery[movement[i,j],j,i]*reporting[movement[i,j]]
      apuse[i,j] <- alive[i,j] + 1
      returned[i,j]~dbern(pcap[apuse[i,j],i,j])
      for (k in 1:4){
        precovery[k,j,i]<-1-exp(-F_at_age[k])
      }
    }
  }
  for (j in first[i]:first[i]) {
    movement[i,j]~dcat(psi[mark_region[i],1:4])
  }
  for (j in second[i]:last[i]) {
    movement[i,j] ~ dcat(psi[movement[i,j-1],1:4])
  }
}
}
}

```

PSAT Model

```

model
{
  for (i in 1:pntags){
    pmovement[i,1]~dcat(ppsi[pmark_region[i],1:4])
    # Model the state transitions
    for (j in 1:plast[i]){
      preturned[i,j]~dbern(popup) }
    for (j in 2:plast[i]) {
      pmovement[i,j] ~ dcat(ppsi[pmovement[i,j-1],1:4]) #psi[p,s] is the probability of moving
      from region p to region
    }
  }
  ##priors:#
  popup~dbeta(0.5,0.5)
  for(p in 1:4){
    psi[p,1:4] ~ ddirch(alpha[p,1:4])
    for (n in 1:4){
      ppsi[n,p]<-psi[n,p] } }
  for (i in 1:ntags){

```

```

#calculate their survival
for (j in second[i]:last[i]){
#first is their first release, can be years 1 2 or 3, this is to calculate survival, second is
first+1, last is the last year at large
alive[i,j]~dbern(survival[acuse[i,j-1],i,j-1])
}
for(j in first[i]:last[i]){
acuse[i,j]<-alive[i,j]+1
survival[1,i,j]<-0
survival[2,i,j]<-exp(-M) #if you are alive, then survival rate
pcap[1,i,j] <-0 # If dead, then you are unavailable for capture
#if you are alive, then state (movement) dependent probability of recapture
pcap[2,i,j]<-precovery[movement[i,j],j,i]*reporting[movement[i,j]]
##asuse[i,j] and apuse[i,j] tells us if the fish is alive or not (1 if alive, 2 if dead)
apuse[i,j] <- alive[i,j] + 1
returned[i,j]~dbern(pcap[apuse[i,j],i,j])
#write out the probabilities of being recaptured: for recovery region, year j, and
individual i
for (k in 1:4){
precovery[k,j,i]<-1-exp(-F_at_age[k])
}
}
for (j in first[i]:first[i]) {
movement[i,j]~dcat(psi[mark_region[i],1:4])
}
for (j in second[i]:last[i]) {
movement[i,j] ~ dcat(psi[movement[i,j-1],1:4]) #psi[p,s] is the probability of moving
from region p to region
}
}
M~dunif(0,10)
for (j in 1:4){
F_at_age[j]~dunif(0,10)
}
}

```


APPENDIX C: CHAPTER 3 ALTERNATIVE MODEL RESULTS

Table C1. Parameters used to populate the tagging model (Actual) and estimates, percent biases, and CVs for the model with half of the DST returns than expected and the PSAT tagging model for yellowfin tuna.

	PSAT Model				DST Model (reduced)		
	Actual	Estimate	Percent Bias	CV	Estimate	Percent Bias	CV
F Region 1	0.18	0.13	-27%	0.03	0.13	-27%	0.03
F Region 2	0.21	0.16	-25%	0.05	0.16	-25%	0.05
F Region 3	0.18	0.14	-24%	0.04	0.13	-25%	0.04
F Region 4	0.08	0.06	-26%	0.07	0.06	-25%	0.06
M	0.6	0.73	22%	0.02	0.73	22%	0.02
P[1,1]	0.948	0.95	0%	0.00	0.95	0%	0.01
P[1,2]	0.05	0.04	-14%	0.10	0.05	-7%	0.09
P[1,3]	0.001	0.002	123%	0.44	0.002	126%	0.45
P[1,4]	0.001	0.002	150%	0.66	0.006	498%	0.42
P[2,1]	0.05	0.03	-36%	0.11	0.04	-28%	0.11
P[2,2]	0.6	0.68	13%	0.03	0.68	14%	0.03
P[2,3]	0.15	0.12	-20%	0.07	0.12	-19%	0.07
P[2,4]	0.2	0.17	-15%	0.10	0.16	-20%	0.10
P[3,1]	0.001	0.002	58%	0.49	0.002	64%	0.49
P[3,2]	0.15	0.13	-16%	0.07	0.13	-17%	0.07
P[3,3]	0.799	0.82	3%	0.01	0.84	5%	0.01
P[3,4]	0.05	0.05	-2%	0.17	0.04	-24%	0.22
P[4,1]	0.001	0.001	-23%	0.73	0.001	16%	0.56
P[4,2]	0.2	0.19	-7%	0.06	0.18	-9%	0.06
P[4,3]	0.05	0.04	-24%	0.12	0.03	-32%	0.13
P[4,4]	0.749	0.78	3%	0.02	0.78	4%	0.02

Table C2. Parameters used to populate the tagging model (Actual) and estimates, percent biases, and CVs for the model with half of the DST returns than expected and the PSAT tagging model for bigeye tuna.

	DST Model (Reduced)				PSAT Model		
	Actual	Estimate	Percent Bias	CV	Estimate	Percent Bias	CV
F Region 1	0.24	0.17	-28%	0.03	0.20	-17%	0.03
F Region 2	0.24	0.23	-6%	0.04	0.20	-17%	0.04
F Region 3	0.12	0.20	-20%	0.04	0.10	-20%	0.04
F Region 4	0.12	0.11	-7%	0.06	0.11	-9%	0.05
M	0.4	0.54	34%	0.02	0.54	34%	0.02
P[1,1]	0.749	0.82	9%	0.01	0.81	9%	0.01
P[1,2]	0.2	0.16	-21%	0.05	0.16	-22%	0.05
P[1,3]	0.001	0.002	143%	0.43	0.001	41%	0.57
P[1,4]	0.05	0.02	-56%	0.20	0.03	-44%	0.16
P[2,1]	0.2	0.15	-27%	0.06	0.15	-27%	0.05
P[2,2]	0.65	0.75	15%	0.02	0.75	15%	0.02
P[2,3]	0.05	0.04	-25%	0.12	0.04	-26%	0.12
P[2,4]	0.1	0.07	-32%	0.11	0.07	-29%	0.11
P[3,1]	0.001	0.0008	-16%	0.58	0.001	8%	0.50
P[3,2]	0.05	0.03	-45%	0.10	0.03	-45%	0.10
P[3,3]	0.749	0.85	13%	0.01	0.84	13%	0.01
P[3,4]	0.2	0.12	-39%	0.09	0.13	-36%	0.08
P[4,1]	0.05	0.03	-40%	0.11	0.03	-38%	0.10
P[4,2]	0.1	0.07	-27%	0.07	0.07	-27%	0.07
P[4,3]	0.2	0.15	-23%	0.07	0.16	-22%	0.07
P[4,4]	0.65	0.74	14%	0.02	0.74	14%	0.02

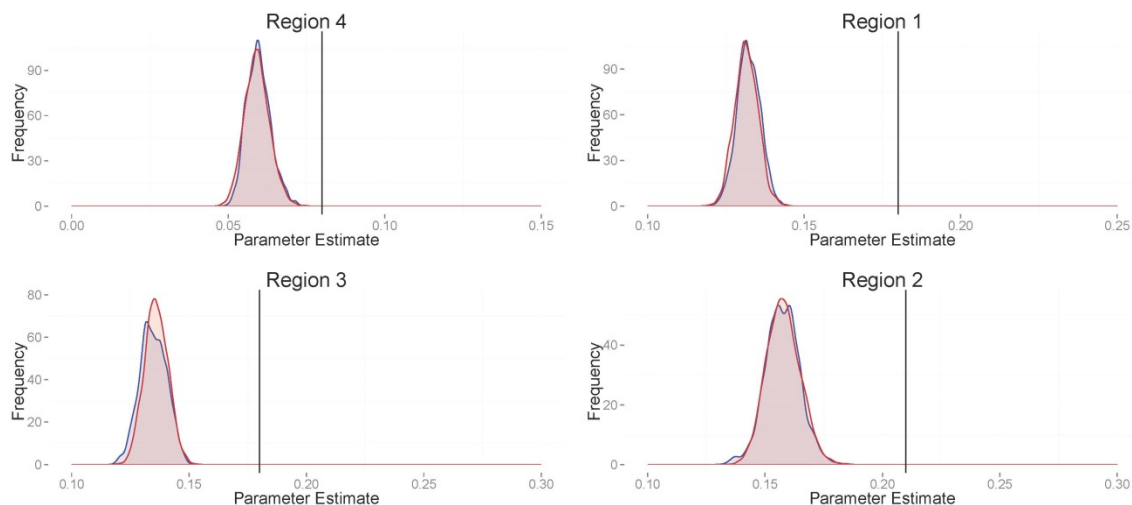


Figure C1. Yellowfin tuna fishing mortality posterior probabilities from the model using conventional tags combined with each of the electronic tags with DST return rates cut in half to estimate movement rate. Blue represents the reduced DST model, red represents the PSAT model and the black line indicates the actual value used to populate the simulation.

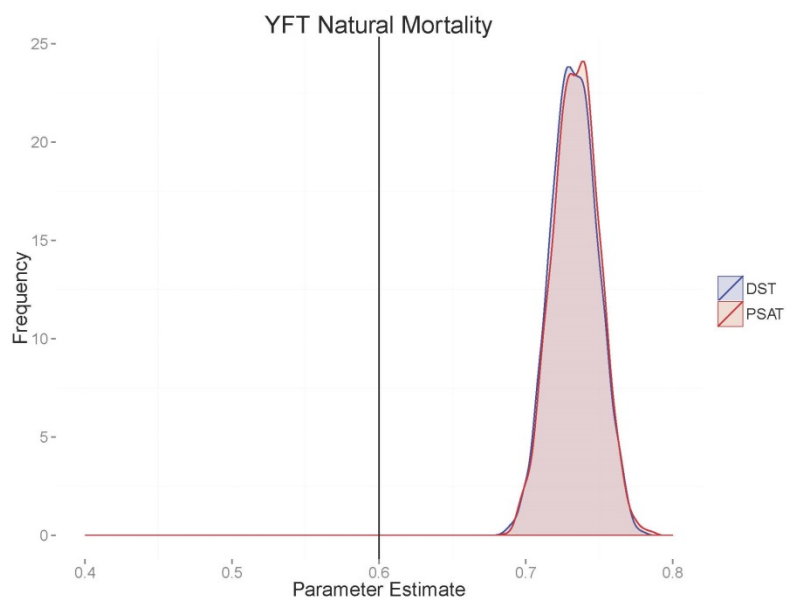


Figure C2. Yellowfin tuna natural mortality posterior probabilities from the model using conventional tags combined with each of the electronic tags with DST return rates cut in half to estimate movement rate. Blue represents the reduced DST model, red represents the PSAT model and the black line indicates the actual value used to populate the simulation.

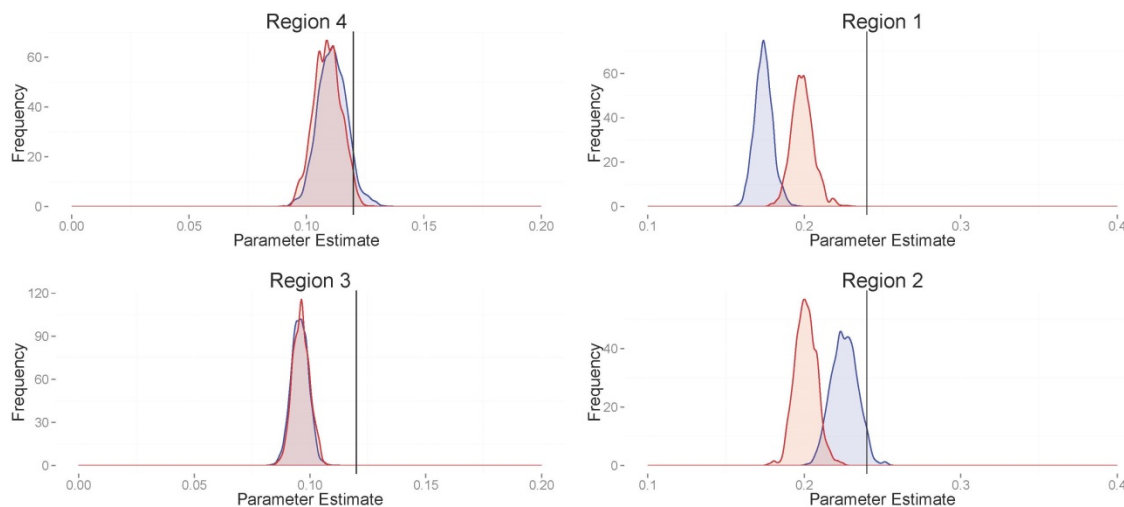


Figure C3. Bigeye tuna fishing mortality posterior probabilities from the model using conventional tags combined with each of the electronic tags with DST return rates cut in half to estimate movement rate. Blue represents the reduced DST model, red represents the PSAT model and the black line indicates the actual value used to populate the simulation.

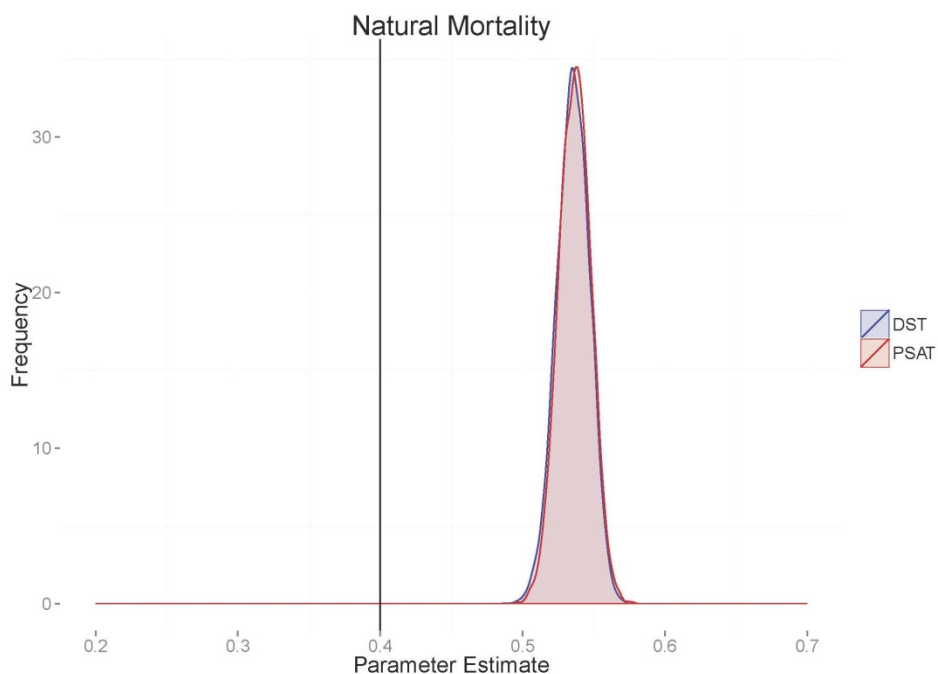


Figure C4. Bigeye tuna fishing mortality posterior probabilities from the model using conventional tags combined with each of the electronic tags with DST return rates cut in half to estimate movement rate. Blue represents the reduced DST model, red represents the PSAT model and the black line indicates the actual value used to populate the simulation.

APPENDIX D: OPENBUGS CODE FOR THE BAYESIAN AGE-SPECIFIC SPACE STATE MODEL DESCRIBED IN CHAPTER 4

```

model
{
for (i in 1:ntag){
#calculate their survival
for (j in second[i]:lasti[i]){
#first is their first release, can be years 1 2 or 3, this is to calculate survival, second is
first+1, last is the last year at large
#for each age, a different survival value
alive[i,j]~dbern(survival[asuse[i,j-1],i,j-1])
##asuse[i,j] and apuse[i,j] tells us if the fish is alive or not (1 if alive, 2 if dead)
}

for(j in first[i]:last[i]){
asuse[i,j]<-alive[i,j]+1 #1 if dead and 2 if alive
survival[1,i,j]<-0 #if dead, stays dead
survival[2,i,j]<-exp(-(TermM*(Lreference/L[age[i,j]]))) #if you are alive, then age
dependent survival rate
pcap[1,i,j] <-0 # If dead, then you are unavailable for capture
#if you are alive, then age and state (movement) dependent probability of recapture
pcap[2,i,j]<-precovery[movement[i,j],j,i]*reporting[movement[i,j]]
apuse[i,j] <- alive[i,j] + 1
returned[i,j]~dbern(pcap[apuse[i,j],i,j])
#write out the probabilities of being recaptured: for recovery region k, year j, and
individual i
for (k in 1:4){
precovery[k,j,i]<-1-exp(-F_at_age[age[i,j],k])
}
}
# Model the movements
for (j in first[i]:first[i]) {
movement[i,j]~dcat(psi[mark_region[i],1:4]) #Fish can move in the first year
}
for (j in second[i]:last[i]) {
movement[i,j] ~ dcat(psi[movement[i,j-1],1:4]) #psi[p,s] is the probability of moving
from region p to region
}
}
for (i in 1:maxage){
L[i]<-97.258*(1-exp(-(0.251*number[i]))) #SKJ growth model
L[i]<-217.3*(1-exp(-0.18*(number[i]+0.709))) #BET growth model
L[i]<-192.4*(1-exp(-0.37*(number[i]+0.003))) #YFT growth model
#number is a vector with a sequence from 1:maxage to calculate length at age
}
}

```

```
##priors:
for(p in 1:4){
  psi[p,1:4] ~ ddirch(alpha[p,1:4])
}
TermM~dunif(0,10)
for (i in 1:maxage){
  for (j in 1:4){
    F_at_age[i,j]~dunif(0,10)
  }
}
}
```