Somatic condition, growth and distribution of Atlantic bluefin tuna (Thunnus thynnus) in the Gulf of Maine

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SOMATIC CONDITION, GROWTH AND DISTRIBUTION OF ATLANTIC BLUEFIN TUNA (THUNNUS THYNNUS) IN THE GULF OF MAINE

BY

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THESIS

Submitted to the University of New Hampshire
In Partial Fulfillment of
The Requirements for the Degree of

Doctorate of Philosophy
In
Zoology

May, 2010
This thesis has been examined and approved.

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5/10/2010 Date
DEDICATION

This dissertation is dedicated to several people who have been a consistent pillar of support throughout my life and who encouraged me to pursue my educational goals. First, to my parents who brought me up in an environment which fostered a love for the outdoors, both in the woods and on the ocean where I was free to explore and ask that most prominent of scientific questions “why?” Thanks for always being there to help me through all of the ups and downs which life has thrown my way and supporting me in this educational pursuit of excellence. Second, to my wife Tracee who met me at the very beginnings of my educational journey and has stayed the course ever since. You have sacrificed so much to see that I obtain this milestone and I appreciate all of your efforts. Thanks for the encouragement, support and love which you have consistently given over the past six years and the persistence to see this out to the end. I am forever indebted to you for all that you have done and sacrificed. Finally, to Bill Millette, Louis Golet, Mort Sweetser, and John Folia, family members that are no longer with us, but who would have been so very proud of this accomplishment and who held such important places in my life.
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ABSTRACT

SOMATIC CONDITION, GROWTH AND DISTRIBUTION OF ATLANTIC BLUEFIN TUNA (THUNNUS THYNNUS) IN THE GULF OF MAINE

by

Walter J. Golet

University of New Hampshire, May, 2010

Atlantic bluefin tuna (Thunnus thynnus), a highly migratory apex predator, utilize temperate feeding grounds to place their tissues into positive lipid balance following reproduction and subsequent migration to northern latitudes. Commercial fishermen target Atlantic bluefin tuna between June and October, but landings have declined 70% from 2004-2009 suggesting adult bluefin tuna may no longer be utilizing the Gulf of Maine as a foraging ground. A series of linear and additive models fitted to multiple fishery dependent datasets identified significant declines in the somatic condition of Atlantic bluefin tuna in the Gulf of Maine. Significant changes in the somatic condition of Atlantic herring, increases in the landings of the commercial herring fleet and changes in Atlantic herring gonad size were also identified. New growth parameters were estimated for Atlantic bluefin tuna sampled in the western Atlantic and these are significantly different than previous estimates for bluefin tuna greater than eight years of age. Finally, there has been a significant shift in the distribution of Atlantic bluefin tuna surface schools greater than 350 kilometers to the east over the past 28 years. Significant associations between Atlantic bluefin tuna and Atlantic herring schools were also identified, but long-term shifts in Atlantic herring distributions did not follow the same
trend as Atlantic bluefin tuna. These results suggest bottom-up and top-down mechanisms are responsible for the changes in somatic condition and distribution of Atlantic bluefin tuna in the Gulf of Maine.
Biology

The northern Atlantic bluefin tuna (*Thunnus thynnus*), a highly migratory pelagic species, is the largest and most evolved of all the scombrids. The complete internalization of red muscle (Sharp 1978), specialized countercurrent retial heat exchanger (Carey and Teal 1966; Carey and Teal 1969; Carey and Lawson 1973), high aspect ratio lunate shaped tail (Marshall 1971, Magnuson 1978), large gill surface area (Muir and Hughes 1969), and specialized pathways for blood flow (Muir and Brown 1971) provide northern Atlantic bluefin tuna (ABFT) with the physiological and morphological adaptations necessary to cross ocean basins and exploit sub-tropical to cold temperate regions inaccessible to many other large pelagic fish. Corrected for size and temperature, tunas have higher standard metabolic rates than other active fishes (Korsmeyer and Dewar 2001). This elevated metabolism, while beneficial for migration and growth, comes at a high cost. In order to maintain elevated levels of somatic and gonadal growth, tunas must consume large quantities of high caloric prey (Crane 1936, Butler 1974). Such requirements present a large biological challenge for most tuna species, which typically inhabit the energy poor pelagic environment of the world’s oceans where aggregations of prey are patchy and highly variable in space and time (Lehodey et al., 2008, Lehodey et al., 2006). However, unlike tropical tunas, ABFT possess the ability to exploit very productive temperate waters that often support a large biomass of high energy prey such as Atlantic herring (*Clupea harengus*) and Atlantic
mackerel (*Scomber scomber*) (Bigelow and Schroeder 1953). The capacity to store large quantities of lipids for migration coupled with distinctive physiological and morphological adaptations provides ABFT with tremendous horizontal and vertical range. However, these same adaptations have made ABFT highly desirable and accessible to many different fishing fleets across the Atlantic for more than two millennia (Doumenge 2000, Desse and Desse-Berset 1994).

**Problem and Significance**

Over the past two decades, demand for large (>180 cm CFL) high quality ABFT have continued to increase as raw fish markets in the United States and European countries continues to grow. Rising global demand, coupled with some extremely high market prices has made ABFT the most valuable fish in the ocean (Bestor 2004). Improved technological advances in gear have placed significant pressure on remaining stocks and currently, ABFT are exploited year round throughout their entire range (Bard 1981, Mather et al., 1995, Liorzou 2001, Pusineri et al., 2002, Bregazzi 2004, Fromentin and Powers 2005, Fromentin and Ravier 2005, Porch 2005).

As a result of such high exploitation, western Atlantic spawning stock biomass (SSB) of ABFT is estimated to be 19% of its pre 1975 level as of 2006 (Fig. 1). Short-term projections through 2009 with a TAC of 2,100 metric tons would increase SSB by just 1.5% per year assuming stable recruitment levels (ANON 2007). From the 1980's thru 2007 Japan, Canada and the U.S. have caught greater than 95% of the western Atlantic quota. The U.S. accounts for 58% of the combined western cumulative catch. Thus, virtual population assessment (VPA) projections for the western Atlantic are strongly influenced by U.S. catch per unit effort (CPUE) indices (only one of eleven,
larval survey is fishery independent). For the past four years, the U.S. has failed to fill its commercial (fish >185 cm curved fork length (CFL)) quota landing approximately 20-30% of its allocated purse seine, general and harpoon category allocation despite the removal of control measures (i.e. closed days, daily retention limits). Landings have successively declined each year, but have remained stable or increased in adjacent shelf regions (Fig 2), (McAllister et al., 2008).

Fig 1. Estimated spawning stock biomass of Atlantic bluefin tuna in the western Atlantic calculated from the 2007 ICCAT bluefin tuna assessment. Current levels of spawning stock biomass are estimated to be approximately 19% of the pre 1975 levels. Despite a rebuilding plan implemented in 1998, spawning stock biomass has remained relatively unchanged (ICCAT 2009 Assessment).
Despite the fact that Japanese and Canadian CPUE’s are stable or increasing, the
decline in the U.S. fishery has led ICCAT’s Standing Committee on Research and
Statistics (SCRS) to recommend a reduction to the western Atlantic TAC through 2009,
and prompted heavy support for a CITES (Convention on International Trade in
Endangered Species) Appendix One listing proposal to curb “out of control” catches in
the eastern stock and help facilitate recovery throughout the Atlantic. In the western
Atlantic, the proposed reduction in catch levels is a precaution being taken under the
view that the decline in the U.S. CPUE is due to a reduction in spawning stock biomass
for the western Atlantic stock. Reliance on CPUE, especially for highly migratory
species can provide unreliable estimates of stock abundance due to the complexities in
fleet dynamics and regulatory measures (Stocker and Hilborn 1981, Hilborn and Walters
1992, Hilborn et al., 2003, Hilborn et al., 2005, Branch et al., 2006) Therefore, it is
prudent to investigate whether the decline in U.S. catch is due to overexploitation or a
result of spatial shifts in distribution/migration in response to changes in environmental
conditions, prey availability, condition or distribution in the Gulf of Maine region.
Fig 2. Annual landings of Atlantic bluefin tuna from the United States, Canada and Japan complied from the NMFS and ICCAT databases. Landings for the U.S. have declined substantially since 2004 while those from the Canadian and Japanese fleets have remained relatively stable and in some regions slightly increased since annual TAC’s were imposed in 1981. Catch per unit effort in the Gulf of St. Lawrence fishery is currently the highest in history (ICCAT catch database).

Distribution in the Western Atlantic

Knowledge of the distributions of ABFT is based largely on historical catch records from artisanal, commercial or recreational fisheries. These records indicate that
ABFT have been observed or captured from Newfoundland to Brazil in the western Atlantic, and from Norway to the northern coast of Africa including the Mediterranean Sea in the eastern Atlantic (Hamre 1958:1960, Hamre et al., 1968, Gibbs and Collette 1967, Baglin et al., 1978, Tiews 1978 Mather et al., 1995). Though fishing effort and gear modifications have expanded rapidly, the majority of fishing effort for ABFT is still concentrated inside the continental shelf margin, resulting in perceived distributions in these regions. However, longline catches and reporting locations from PSAT (pop-up satellite tags) have shown a continuous distribution of ABFT across much of the central north Atlantic (Murray 1953; Wilson 1960; Shingu and Hisada 1977; Mather et al., 1995 Lutcavage et al., 1999; Block et al., 2001; Lutcavage and Luckhurst 2001; Block et al., 2005, Galuardi et al., in press) illustrating their utilization of distant water pelagic environments. Spatial and temporal distributions of ABFT are size dependent, likely resulting from changes in migration brought about by life history requirements (i.e. feeding and reproduction) and physiological limitations (Mather et al., 1995). Compared with other tunas, ABFT undertake extensive seasonal migrations (Rivas 1955; Mather et al., 1995; Block et al., 2001, Wilson et al., 2005; Block et al., 2005) to satisfy somatic and reproductive requirements. In the western Atlantic, sexually mature ABFT are known to spawn in and around the Gulf of Mexico/Straits of Florida from April to June (Rivas 1954, NRC 1994, Mather 1995, Nemerson et al., 2001, Block et al., 2005). Disbursed across the continental shelf break, post spawning individuals migrate northward and distribute themselves on the northwest Atlantic shelf from the mid-Atlantic Bight to Newfoundland (Mather et al., 1995, Block et al., 2001, 2005, Wilson et al., 2005, Sibert et
al., 2006, Galuardi et al., in press) where they spend up to six months replenishing depleted lipid reserves.

Within the Gulf of Maine, large medium and giant (>185 cm CFL) ABFT begin to exploit the productive feeding grounds in May-June (Crane 1936; Bigelow and Schroeder 1953; Mather et al., 1995) and individuals continue to enter this region through early July at which point larger schools aggregate on prominent bathymetric features such as Platts and Stellwagen Banks, Jeffries Ledge, the Great South Channel and George’s Bank by late July and August (Lutcavage and Kraus 1995; Lutcavage et al., 1997; Schick et al., 2004). Complete dispersal of the New England and Canadian assemblage from this region occurs by late November (Wilson 1960; Lutcavage and Kraus 1995; Lutcavage et al., 2001; Wilson et al., 2005) with schools presumably en route to alternative feeding (Butler 2007) and (southern) spawning grounds. Reconstructed migration routes from seven years of electronic tagging (1997-2003) in the New England region shows a high degree of inter-annual variation in migration patterns to and from this region (Lutcavage et al., 1999; Block et al., 2001; Wilson et al., 2005; Block et al., 2005; Sibert et al., 2006, Galuardi et al., in press) both supporting and contradicting the traditional migration paradigm for the western Atlantic stock and leaving considerable questions about their stock structure, annual mixing rates and inter-annual distributions which are not answered by historical fishing patterns (Galuardi et al., in press).

History of the Fishery

The ABFT has been harvested in the eastern Atlantic and Mediterranean Sea since the seventh millennium BC where Phoenician, then Roman fishermen captured them enroute to the spawning grounds (Desse and Desse-Berset 1994, Doumenge 2000).
Primitive gears such as handlines, beach seines and traps remained unchanged and served as the primary methods of harvest until the 20th century. Rapid technological advancements post WWII led to the development of the commercial purse seine followed by distant water longliners in the early 1950's (Shiohama et al., 1965). Expansion of the fleets was rapid and catches increased substantially due to fishing in previously unexploited regions of the bluefin’s range.

In contrast to the eastern Atlantic and Mediterranean, ABFT fisheries in the western Atlantic are less than a century old. Initial sport fisheries were developed in the early 1930’s off Wedgeport Nova Scotia, Casco Bay Maine and Ipswich Bay Massachusetts (Farrington 1939, 1949a, 1949b) where bluefin were landed as part of annual tournaments. Post WWII popularity of these tuna tournaments expanded throughout New England, with minimal catches of no more than a few hundred fish annually. Experimental purse seine fisheries during 1951 and 1954 in and around Cape Cod Bay initiated the commercial purse seine fishery in 1958 (Squire 1959). High catches of small and medium fish caused a rapid expansion in effort and by 1964, 21 vessels landed 5,600 metric tons (mt) of small ABFT between Cape Hatteras N.C. and Cape Cod, M.A. (Wilson 1965). A pronounced shift in targeting strategies by fishing fleets was precipitated in 1972 by Japanese buyers paying premium prices for late season, high fat content, large ABFT (>180 cm CFL). As a result, effort in all categories (e.g. purse seine, harpoon, rod & reel, longline) rapidly increased across the western Atlantic and shifted fishing pressure towards the older age structured portion of the stock. Surprisingly, throughout much of its history, the bluefin fishery remained largely unregulated until 1974, when the state of Massachusetts restricted the number of large
bluefin tuna landed in state waters. Beginning in 1975, annual quotas were imposed and landings were restricted at the federal level.

However, the highly migratory nature of ABFT made national management strategies difficult and ineffective, thus even federal management policies were inadequate (Mather et al., 1995). Cooperation at the international level began in the mid 1970's with the formation of the International Commission for the Conservation of Atlantic Tunas (ICCAT). This organization was granted the authority by signatory nations to oversee the management of Atlantic tunas and tuna like species. As required, signatory countries are obligated to report catch statistics and research results to the commission for evaluation and inclusion in stock assessments (Miyake 1975, Caddy and Burnett 1976, Kume 1976, 1977). Initial assessments were conducted under a one stock hypothesis in the early 1970's. However, growing political pressure and statistical convenience prompted the consideration of a two stock hypothesis in 1976 (Whynott 1995, Fromentin and Powers 2005). In 1980, ICCAT adopted this hypothesis and established a management boundary at 45° W, dividing the ABFT population into separate stocks, western and eastern Atlantic, and calculated separate spawning stock biomass estimates (Parrack 1980, 1982). Scientific data supporting this division were the occurrence of small to large size classes in both management areas (Bigelow and Schroeder 1953, Wilson 1965, Hamre et al., 1968, Hamre et al., 1971, Shingu et al., 1975, Tiews 1978), separate spawning grounds in the Mediterranean Sea and the Gulf of Mexico (Sella 1924, 1930, Scaccini 1965, Juárez 1974b, Richards 1976, Montolio and Juárez 1977), no known spawning in the central Atlantic, low levels of mixing (from conventional tagging) (Brunenmeiser 1980), significant differences in presumed size at
maturity (Tiews 1963, Rodriguez-Roda 1964, Westman and Neville 1942, Turner et al., 1991, Mather et al., 1995), substantial differences in estimated SSB (Parrack, 1980, 1982, Powers et al., 1983) and the lack of continuity in catches across the central north Atlantic. However, accumulated scientific evidence during the past two decades indicates this simple management strategy may no longer be appropriate (Fromentin and Powers 2005, Fromentin 2008, Galuardi et al., in press). This includes similarities in growth rates between the stocks, annual mixing on the foraging grounds (Block et al., 2001, Lutcavage et al., 2001 Block et al., 2005), the continuous distribution of catches by Japanese longliners across the central north Atlantic starting in the 1990’s (Miyabe and Hiramatsu 1994, Olafsdottir and Ingimundardottir 2000) and the possibility that western ABFT mature and spawn at a younger age (Goldstein et al., 2007) than current management assumptions (Turner et al., 1991, Diaz and Turner 2007). Nonetheless, under the most current assessments (ANON 2008), ICCAT continues to allocate separate east and west quotas with large differences between the respective TAC’s (2,100 mt west and 28,500 mt east). These assessments utilize eleven indices of abundance to establish numbers of fish at age, but only the larval survey in the Gulf of Mexico is fishery independent and only a few larva are typically captured. Thus, assignment of these quotas is highly dependent on landings trends observed within each region. As a consequence, spatial shifts in distribution of local assemblages could impart a serious bias with regards to understanding of population level trends (Hilbron and Walters 1992) since distributions may shift across international boundaries or to distant pelagic environments beyond the reach of local fishing fleets.
The Gulf of Maine Fishery

The western Atlantic allocation is shared by the United States, Canada, and the Japanese long-line fleet which, collectively landed between 2,000 and 16,000 metric tons annually throughout the fisheries history (Fig 3). The U.S. and Canada have concentrated fisheries inside the continental shelf (typically <150 km from shore) with minor contributions from distant long line vessels (Clay et al., 1984, Clay and Hurlbut 1989, Mather et al., 1995), while Japanese longliners target fish outside the EEZ to the 45° W management boundary (Miyabe and Hiramatsu 1994, Mather et al., 1995, Olafsdottir and Ingimundardottir 2000). Initial allocations of annual quota between nations were based on historical levels of catch while current quotas are implemented based upon the most recent assessments (ANON 2003, ANON 2007). Catches of ABFT prior to quota implementation varied considerably due to a lack of regulation, but since 1980, TAC’s have been landed or slightly exceeded (ANON 2009). The shift in targeting practices to older age classes produced a typical exploitation pattern as recorded by landing statistics over the past 28 years. Initial fishery removals were dominated by the largest size classes and subsequent removal of younger age classes occurred each year (Fig 4) until 1994. A large cohort of large medium (178-195 cm CFL) ABFT recruited to the commercial fishery in the early 1990’s and appears to have sustained the fishery between 1994 and 2003. However, there are no signals in the recorded data to suggest another cohort of large medium ABFT recruited to the fishery (Fig 5). In 2003, a binomial distribution of size classes suggested that another cohort of ABFT may be recruiting to the commercial fishery; however, subsequent landings between 2004 and 2008 did not show this trend. As a consequence, landings of commercial fish have been suppressed (collective landings
<35% of TAC) since 2004 (Restrepo 2009). It should be noted that catches in 2009 were approximately 30-40% higher than the previous four years for the harpoon and general category, but the total landings (~250 mt) for the general category were still only 33% of the total yearly allocation. In addition, only one of the five pure seine vessels has been successful in capturing ABFT since 2005. It is important to note that reductions in landings combined with increased trip costs (fuel) have reduced overall effort during the past five years. However, an increase in relative abundance of younger year classes is evident in the catch data (Brown 2009) suggesting the possibility of stronger recruitment in future years provided these year classes demonstrate feeding site fidelity to the Gulf of Maine. Electronic tagging (Galuardi et al., in press) suggest high site fidelity to the northwest foraging grounds, but stock composition (east vs west origin) complicates efforts to forecast future recruitment to the commercial fishery (Rooker et al., 2006a, Dickut et al., 2009).
Fig 3. Landings of Atlantic bluefin tuna in the western Atlantic by all gear types from the U.S., Canadian, and Japanese fishing fleets. Stabilization of the catches post 1980 results from quotas implemented by ICCAT. The large increase in landings during the 1960’s results from the “Brazilian Episode” and U.S. seiners targeting juvenile Atlantic bluefin tuna (ICCAT catch database).
Fig 4. Median lengths and weights of Atlantic bluefin tuna landed in the Gulf of Maine. Note, only general category (rod and reel fish) data have been used in this dataset. Harpoon and purse seine regulations impose a 206 cm CFL minimum size limit with a 15 percent underage allowance. Thus, sampling is biased towards larger fish and would likely under estimate numbers of smaller size classes (e.g. 185-205 cm CFL). General category data provide a more robust estimate of size class distribution by reducing this size bias. General category landings represent approximately 60% or greater of the annual allocated quota (Landings data from the NMFS HMS Division, Gloucester, MA).
Fig 5. Length frequency distributions for Atlantic bluefin tuna landed in the Gulf of Maine by the general category commercial sector from 1980-2007. A cohort of Atlantic bluefin tuna recruited to the fishery in 1994 and sustained the fishery through 2003, but subsequent cohorts have not entered the fishery and catch levels have declined since 2003 (Data source NMFS HMS Division Gloucester, MA).

Changes in Regional Abundance

Atlantic bluefin tuna migrations are complex with a large degree of intra and inter-annual variability (Lutcavage et al., 1999, Block et al., 2001, Block et al., 2005, Sibert et al., 2006) expressed by age class and between tagging regions. Oceanographic and biological drivers of this variability are poorly understood, particularly at the regional
scale (Schick et al., 2004). Despite the complexity at the regional level, broad scale classifications have been applied to classify tuna migrations as directed or passive (Nakamura, 1969). Direct migrations result from pronounced shifts in physiological requirements, such as spawning in subtropical regions and feeding in temperate high latitudes (Rivas 1955, Tiews 1978, Clay et al., 1984, Mather et al., 1995) often occurring on an ocean basin scale. Directed migrations are energetically costly (Nottestad et al., 1999) and involve considerable risk in terms of mortality or reduced fitness, so the benefits to the population over time (i.e. increased larval survival, rapid lipid accumulation) must remain positive for individuals to annually return (Slotte and Fiksen 2000). Passive migration is more spatially restricted than directed, and occurs in response to localized changes in oceanography (e.g. SST, fronts, currents) or biological factors (e.g. prey distributions). Spatial and temporal fluctuations in the abundance and distribution of ABFT at varying scales are well documented throughout their range (Tiews 1978, Clay 1989, Mather et al., 1995, Ravier and Fromentin 2001; 2004;2008). Despite large historical shifts in distribution (e.g. Nordic fishery, Brazilian episode), broad scale migration patterns to the northwest Atlantic feeding grounds (using landings as a metric) appear to be unchanged over the past half century. That is to say, some component of the Atlantic stock migrates annually to this region in order to replenish depleted energy reserves. The origin and composition of this assemblage may in fact have changed, but ABFT are still utilizing this region and have not completely shifted distribution as they have elsewhere (Fromentin 2008). While the large-scale spatial and temporal distributions of ABFT on the feeding grounds in the western and eastern Atlantic have been predictable (ANON 2003;2007;2009), decadal shifts in regional
abundance (e.g. Newfoundland, Gulf of St. Lawrence) have also occurred at specific locations (Tiews 1962; Caddy and Butler 1976; Tiews 1978; Clay 1989; Mather et al., 1995; Ravier and Fromentin 2001). Abrupt declines in regional abundance of ABFT are not uncommon and likely manifest through changing environmental conditions which influence prey distributions. Clay (1989) suggested changes in migration patterns and lack of recruitment from younger year classes were responsible for the collapse of the Newfoundland and St. Margaret’s Bay fisheries in the 1980’s. Tiews (1978) stated similar reasons for the sudden collapse of the ABFT fisheries in Nordic waters in 1963, but neither author identified specific biological or physical variables responsible for these spatial shifts. In addition to lack of recruitment, landings data provide a compelling argument that increasing effort may have contributed to the Nordic decline (Fig 6). The “Brazilian Episode”, an abrupt emergence and decline (within five years) of large aggregations of ABFT off the coast of Brazil in oceanic waters typically inhabited by tropical tunas (Fromentin and Powers 2005), though not quantitatively linked to the Nordic fishery, exhibited similar ephemeral properties (Fig 7). Pusineri et al. (2002), proposed that Spanish trap catches (coincident with the Nordic collapse) dominated by large adult size classes in the east Atlantic and Mediterranean, resulted from lack of recruitment or overfishing, while others have linked declines in regional abundance to environmental factors (Marsac 1999; Ravier and Fromentin 2004). Due to the time period in which they occurred and the inherent difficulties in quantifying distant water fisheries, much of these analyses have been retrospective in nature, and drew conclusions based on limited data (Fromentin 2008). Though there have been small changes in some regional fisheries throughout the Atlantic it has been several decades since an abrupt
decline at a regional scale has been observed on a major fishing ground such as the one which has occurred in the Gulf of Maine beginning in 2004.

Fig 6 Catch and effort data from the Nordic Atlantic bluefin tuna purse seine fishery. The commercial fishery collapsed in 1964 due to declines in abundance. Despite four decades since the fisheries collapse, and a complete reduction of effort, the fish have not returned (Data source ICCAT).
Fig 7 Atlantic bluefin tuna commercial landings for the Nordic and Brazilian fisheries. Though both fisheries were short lived, coincided temporally and were subjected to intense fishing pressure, neither decline has been solely linked to increased effort nor has connectivity between the regions been demonstrated (Data Source ICCAT).

Landings and Somatic Condition in the Gulf of Maine

Historically, the Gulf of Maine and adjacent shelf waters have been the primary commercial fishing ground for ABFT. Throughout the past 50 years, this region has accounted for 79% of US landings. Beginning in 2004 and continuing through 2009, the New England fishery experienced a sharp decline in commercial landings, harvesting only 15-20% of its allocated annual quota share (Fig 8) (http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html).

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Coincident with the apparent decline in availability of ABFT in New England, commercial fishermen and brokers have observed a reduction in the seasonal fattening or somatic condition of ABFT, noting that fish harvested at the end of the season no longer accumulate substantial lipid content. The consequences of this are two-fold. First, lower fat content typically results in reduced monetary returns (Bestor 2004), thus impacting the economies of coastal communities. Second and more importantly, a reduction in somatic and gonadal lipid stores may increase natural mortality, reduce fecundity, shift reproductive patterns and reduce the effectiveness of current fishing controls implemented to rebuild western Atlantic spawning stock biomass of ABFT. Such uncertainties can only have negative consequences, particularly in light of recent assessments which under certain model scenarios (absence of fishing), will still not rebuild the stock by 2019 (ANON 2009).

Preliminary investigations indicate declining somatic condition of ABFT extends along much of the northwest Atlantic shelf (Golet et al., 2007, Neilson et al., 2007) and that while drivers of changing spatial distribution may be unique to U.S. waters, somatic changes are ubiquitous across the northwest Atlantic. While shifting spatial distributions of fish may impact local economies, reduction in lipid reserves can significantly impact several aspects of reproduction (e.g. total egg production, egg quality or skipped spawning) for western ABFT and impart further uncertainty into calculations of spawning stock biomass from VPA analysis used for rebuilding scenarios.

The results of reduced lipid stores have been documented for different species, but within the same shelf system of the northwest Atlantic. For example, Atlantic cod (Gadus morhua) in the Gulf of St. Lawrence experienced a marked decline in somatic
condition which was subsequently linked to lowered fecundity and increased natural mortality (Lambert and Dutil 1997a; Dutil and Lambert 2000; Lambert and Dutil 2000). A reduction in somatic and gonadal condition, recruitment failure coupled with environmental changes and overfishing likely contributed to the early 1990’s collapse of one of the most prolific ground fisheries in the world. Large shifts in condition and distribution of an apex predator such as the ABFT may indicate that a regime shift in the Gulf of Maine has occurred, possibly due to an interruption in the “bottom up” transfer of energy through trophic levels, or through synergistic effects between the environment and current fishing practices at lower trophic levels. Given high metabolic and reproductive demands, coupled with a short temporal window for feeding (3-5 months) ABFT need to optimize their foraging strategies. Energetic thresholds likely modify searching behavior such that insufficient prey (quantity [overall abundance/patch size] and quality) or conversely, large quantities of prey induce different searching modes to find the most suitable habitat (Kvamme et al., 2003). For a long lived species like ABFT, successive years of poor energy acquisition could change migration patterns to favor northern latitude feeding grounds, where prey abundance, condition, or both are greater. Currently, it appears that those ecosystem and or anthropogenic drivers and their residual effects remain at play in the Gulf of Maine, since the commercial ABFT fishery has not recovered to date.
Fig 8 Atlantic bluefin tuna landings for the U.S. commercial fleet. Differences in landings between New England and the remaining states are from juvenile bluefin tuna purse seined off the mid-Atlantic Bight in the mid 1960's and longline catches during the 1970's. Declines in 1982 and 1986 were due to reduced quota share allocated to the U.S. fleets (Data NMFS HMS Division Gloucester, MA).

The nature of the declines in regional abundance and somatic condition, suggest the drivers of these changes are present at multiple scales. Declines in regional abundance of large (>185 cm CFL) ABFT suggest the possibility of a substantial spatial shift in bluefin tuna distribution as a result of; 1) a reduction in spawning stock biomass which, through range constriction has concentrated bluefin tuna in the most preferred habitats or 2) conditions within the Gulf of Maine have changed and no longer sustain the energetic requirements of adult ABFT. Thus, ABFT are forced to disperse to more
favorable regions which produce larger energy stores per unit time. Large assemblages and stable or increasing CPUE directly over the international boundary (ANON 2009, Neilson et al., 2007, McAllister et al., 2008) suggest factors responsible for shifts in distribution may be directly related to conditions in the Gulf of Maine (within U.S. territorial waters). In contrast, somatic changes observed across the northwest Atlantic shelf may indicate restrictions in energetic flow through trophic levels, which are potentially mediated by environmental changes via large scale atmospheric forcing (i.e. climate and oceanographic shifts).

Clearly, there is cause for concern regarding the status of the western Atlantic ABFT stock, particularly since the largest component of the western Atlantic fishery has experienced such a rapid decline in apparent availability. While a reduction in the TAC is the most cautious and easily implemented recourse, it does little to promote our understanding of the spatial and temporal dynamics associated with changes in the northwest Atlantic ABFT assemblages. This complicates management decisions which are unable to distinguish distribution shifts from declines in population abundance. Quantifying these changes in distribution coupled with identification of factors that may be root causes of such shifts will facilitate appropriate management decisions and rebuilding of the western ABFT stock. Collectively, this knowledge will better position the scientific and management community toward achieving successful and sustainable fisheries, and bring us closer to implementing a comprehensive or ecosystem based management strategy for highly migratory species.
Research Objectives

This dissertation is divided into three sections that collectively address observed changes in the distribution and somatic condition of commercial sized ABFT in the Gulf of Maine. Chapter One (Somatic Condition of Atlantic Bluefin Tuna in the Gulf of Maine) presents a quantitative analysis of changes in ABFT somatic condition through the use of qualitative observations and morphometric measurements from landings data. These observations are then fitted to different linear and non-linear regression framework models to support or refute the hypothesis that somatic condition of ABFT has declined. Specific hypotheses relating to shifts in diet composition, prey quality, size and fishing practices of lower trophic levels were tested to identify whether one or more may be causal variables. Chapter Two (Age and Growth of Atlantic Bluefin Tuna in the Western Atlantic) will identify whether changes in somatic condition of ABFT have impacted growth. To accomplish this, a new growth curve was fitted utilizing measurements from dorsal spines collected along the east coast of the United States from 2004-2007. Updated growth curves were compared to previous growth rates estimated for the western Atlantic and to curves in the eastern Atlantic. Chapter Three (Distribution of Atlantic Bluefin Tuna in the Gulf of Maine) will utilize fishery dependent data (commercial catch locations) to examine intra and inter-annual spatial and temporal relationships in Atlantic herring and ABFT distribution in the Gulf of Maine. Specifically, analyses will identify directionality of movement for each species and whether these shifts are linked. This final analysis will also test the hypothesis that areas of high Atlantic herring density also contain higher numbers of ABFT, which may help define whether ABFT distributions in the Gulf of Maine are largely driven by prey aggregations as proposed in Schick et al.
(2004) and Gutenkunst et al (2007). These analyses will provide insight into whether a spatial shift has occurred and its magnitude. My dissertation objectives are to provide new and original research that can quantify the observed changes in somatic condition and spatial distribution of ABFT in the Gulf of Maine while furthering understanding of what drives such complex migratory behavior and what factors may explain the rise and fall of commercial fisheries across the Atlantic.
CHAPTER 1

SOMATIC CONDITION OF ATLANTIC BLUEFIN TUNA IN THE GULF OF MAINE

Abstract

Atlantic bluefin tuna (*Thunnus thynnus*), a highly migratory apex predator, utilize temperate feeding grounds to place their tissues into positive lipid balance following reproduction and subsequent migration to northern latitudes. Seasonal feeding cycles at high latitudes are three to six months, thus ABFT need to optimize feeding strategies to ensure adequate levels of somatic and gonadal energy to support their extensive migratory behavior and substantial reproductive output. Energy budgets are optimized by preferentially feeding on abundant high energy prey such as Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber Scomber*). Despite high abundance of these prey species, commercial fishermen observed changes in somatic condition of ABFT over the past decade. These changes were quantified by fitting commercial landings (length weight ratios) and dealer grade data of ABFT to generalized additive (GAM’s) and multinomial regression models respectively. Significant declines in somatic condition occurred across all size classes (>185 cm CFL) (n=93,914) with a 5-25% decline in total seasonal lipid accumulation from 1980-2007. Additional analyses were conducted to test specific hypotheses which potentially identify anthropogenic and biological drivers of this decline. Significant declines in herring somatic condition, increases in herring gonad weight and trip catches from the commercial herring fleet during June through October (the prime ABFT feeding window) and a stable diet
composition of ABFT during this time period were identified. These results suggest that synergistic effects of biological and anthropogenic drivers may have contributed to this decline. These include perturbations to the bottom up transfer of energy and changes in harvesting practices of commercial fisheries on middle trophic levels (Atlantic herring). Reductions in key energy stores from reduced lipid acquisition can diminish allocations to growth and gamete production which, collectively, can have detrimental consequences on critical life history parameters essential for successful rebuilding of the western Atlantic population.

**Introduction**

The Gulf of Maine/George’s Bank region lies at the southern end of the northwest Atlantic shelf system, an oceanographic transition zone (MERCINA 2001) where colder, sub polar, less saline water masses (primarily from the Labrador Sea) meet temperate, more saline Gulf Stream water masses (Loder et al., 2001). This convergence of water masses makes the region one of the most productive areas of the entire shelf system. Rates of primary productivity in the least productive offshore waters in the Gulf of Maine produce > 270 g C m$^{-2}$ yr$^{-1}$ (O’Reilly and Busch 1984, O’Reilly et al. 1987). These high rates of productivity support a large diversity of species across four trophic levels. However, as with other productive wasp-waist ecosystems, typically only a few species dominate (in terms of abundance and importance to the system) at the mid trophic levels. Examples in the Gulf of Maine include the second order consumer *Calanus finmarchicus* and the tertiary consumer, Atlantic herring (*Clupea harengus*; “herring”). *Calanus finmarchicus* is an expatriate species in the Gulf of Maine/George’s Bank region (Greene et al., 2003) due to advective properties which bring it into coastal shelf systems.
(Longhurst, 1998) where it often dominates the plankton assemblage (Raymont, 1983, van der Spoel & Heyman, 1983, Mauchline 1998). Circulation patterns aggregate *C. finmarchicus* into high density patches which are exploited by several pelagic planktivores, notably herring and the north Atlantic right whale (*Eubalaena glacialis*). Calanus finmarchicus contributions to total stomach volume of herring have exceeded 50% demonstrating preferential feeding (Link and Almeida 2000). *Calanus finmarchicus* lipid volumes can exceed 70% of body volume (Miller et al., 2000). Herring store proportionately more lipids than most schooling pelagic species (Krzynowek et al., 1989, Lawson et al., 1998) and have a seasonal accumulation of lipids which peaks prior to spawning (Engelhard and Heino 2006) making them important sources of lipids for upper level predators during a short high latitude foraging season. Tracking lipid accumulation cycles can provide information on the peak energetic value of individual herring. A mismatch between peak energetic value of prey and predator migration may reduce somatic condition though reduced caloric intake, (Piatt and Anderson 1996) despite equivalent prey consumption. Consequently, in the Gulf of Maine, herring form a critical ecological link between lower (zooplankton) and upper (e.g., marine mammals, ABFT, seabirds) trophic levels (Overholtz and Link 2007, Link and Almeida 2000, Chase 2002, Lavigne 1996).

Atlantic bluefin tuna time their migrations to the Gulf of Maine with the presence of herring schools (Crane 1936) and exploit this prey base beginning in May when fat and energy stores have been reduced (Mourente et al., 2001) and mesenteric lipid stores have been utilized for gametogenesis and subsequent migration to feeding grounds. Atlantic bluefin tuna sampled during the first month of the feeding season are typically
lean, with little to no perigonadal or body fat reserves (Rivas 1955, Estrada et al., 2005; Goldstein et al., 2007). Utilizing visceral retes which warm the stomach (Cary et al., 1971) and digestive enzymes with fast turnover rates (Stevens and McLeese, 1984) ABFT rapidly convert this prey base into somatic lipid stores. Energy allocation in adult ABFT is directed to the intra-musculature or perigonadal lipid stores (Medina et al., 2002, Abascal et al., 2004). Previous estimates of seasonal lipid accumulation calculated increases in body weight of 7-10% per month (Rivas 1955, Butler 1974). The majority of mass gain was reflected in the accumulation of intra-musculature and perigonadal lipid stores, which presumably provide the necessary reserves for migration to the spawning grounds and subsequent gamete production following their departure from the Gulf of Maine in late September to mid November (Lutcavage and Kraus, 1995; Wilson et al., 2005). An outstanding question is whether changes in somatic lipid stores track lipid concentrations in the perigonadal region and whether ABFT maintain the perigonadal lipid stores in the face of declining somatic condition. This is important to note since ABFT may be able to withstand substantial reductions in somatic lipids while still maintaining high reproductive output.

Spawning stock biomass for age 2+ herring in the Gulf of Maine stock complex peaked in 1997 at 830,000 mt and has since fluctuated at that level without trend through 2008 (Shepard et al., 2008). However, 80% of this biomass is located in offshore waters distributed across George’s Bank and portions of Nantucket Shoals. Estimates for the inshore component suggest that up to 18% of the total complex biomass resides in area 1A. Although the inshore component is the smallest portion of the stock, it has received the largest amount of fishing pressure during the past 30 years and typically accounts for
50-90% of the annual TAC (Fig 9). In addition, changes in market demand have altered fishing strategies, which may have led to a disproportionate amount of the inshore

Fig 9 Annual landings of Atlantic herring by the commercial mobile gear (purse seine, trawler) fleet for the Gulf of Maine/George's Bank herring stock complex.
component being landed during summer months, a time period when ABFT rely heavily on high abundant prey. Thus, it is possible that while overall abundance of the stock complex has increased, inshore areas may have experienced regional declines due to the disproportionate amount of annual TAC removed from Area 1A, and the market demand for herring from June-October to support the lobster industry. In higher latitudes of the northwest Atlantic, herring spawning stock biomass is inversely related to gonad size, likely due to density dependent processes (Winters and Wheeler 1993). Therefore, if populations of herring are reduced in Area 1A, selective pressures should promote large energy allocation to gonadal growth and subsequently reproductive output. Such changes in allocation to reproductive output should increase mean gonadal size during the spawning season and could serve as a proxy for whether inshore population abundance has declined.

Recent observations by fishermen, brokers, and co-operative managers have identified two declining trends in the Gulf of Maine commercial ABFT fishery during the past 15 years. The first is an abrupt and continued decline in the abundance of large medium (>175 cm) fish which began in 2004 and continued through the 2009 commercial fishing season. Landings data indicate that no more than 30% of the collective (purse seine, rod and reel, harpoon) allocated ICCAT quota has been captured since 2004 in the Gulf of Maine region (http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html). Aerial surveys between 1994 and 1997 detected hundreds of surface schools annually with up to 5000 adult ABFT in a single school (Lutcavage and Kraus, 1995), illustrating the magnitude and rapidity of this decline. Second, coincident with the reduction in catch, over the past
decade fishermen and dealers reported a decline in fish quality irrespective of season. Thus, fish landed in September and October (typically at the peak of their seasonal fattening cycle) had the same somatic condition as those landed in June, suggesting that ABFT are not establishing the fat reserves of previous decades. Given that energy allocation is a key component of growth, maturation, reproduction, and migration in long-lived fishes (Marshall et al., 1999; Rideout et al., 2005; Jørgenson et al., 2006), a decline in the somatic condition of ABFT would be expected to affect the population via those mechanisms.

Catch rates of highly migratory species, especially ABFT, have fluctuated over the years in many different regions of the world (Anderson and Piatt, 1999; Ravier and Fromentin, 2001). These top pelagic predators have altered their distribution due to environmental shifts (Anderson and Piatt, 1999), or suffered localized depletion due to fishing pressures (Tiews, 1978; Fromentin and Powers, 2005). While these may explain shifts in distribution or abundance of ABFT in the Gulf of Maine, it does not account for the apparent decline in quality of those fish remaining in the area.

This study utilized a variety of field, laboratory, and statistical models to test the following general hypothesis that somatic condition of ABFT has declined. Specific analyses were performed to test whether these declines results from: 1) the “junkfood hypothesis” (displacement of high caloric to low caloric prey), 2) changes in the somatic condition of prey, 3) fishing pressure on lower trophic levels, 4) reduced abundance.
Material and Methods

ABFT Condition Grade Data

Lacking quantitative lipid extraction values, the somatic condition of fish over extended time periods is often interpreted through the use of Fulton’s K or linear regression, both of which give a quantitative value to the physical condition of fish (Cone 1989). Such analyses were not possible in this study because individual lengths and weights were not recorded for many of the fish. As a proxy, we used grade data from brokers in the commercial ABFT fishery who grade every fish before purchase. This procedure is quite involved and often requires schooling or an apprenticeship to learn the trade (Bestor 2004). Grading involves a qualitative assessment of the fish’s condition defined by the characteristics of freshness, color, fat/oil, and shape (Bartram et al., 1996, Bestor, 2004). Fat grade is assessed by evaluating the amount of marbling in a tail cut sectioned between the third and fourth finlet, the thickness of the midsection, and the amount of fat present in a small core of muscle biopsied near the fish’s mid-line. Shape grade is determined by the overall appearance of the fish, the more rotund the better. A good quality fish will receive high marks in all categories. Even though different graders may use different terms, ranking of fish quality is consistent between experienced graders (Foote¹).

Two separate ABFT grade databases were collected; the first from a single tuna grader at the Yankee fishermen’s cooperative with 20 years experience in the fishery and the second from the National Marine Fisheries Service (NMFS) dealer reports archive. For both datasets fat/oil content and shape were used as proxies for fish condition. Fish

with large fat reserves and rotund appearance are presumably feeding in excess of their
daily metabolic requirements and hence, are in good condition. Fat/oil content and shape
are reasonable proxies to assess condition since unlike freshness and color, they cannot
be altered by either the time fishermen are at sea or type of gear used for harvest. For the
first dataset, individual grades were transcribed from logbooks. A total of 3,834 fat and
3,082 shape observations were complied from 1991 to 2004. Grading was carried out by
the same individual utilizing the same grade scale for the 14 year period utilizing fine
grades. Fish ranged in size from the commercial minimum of 185-300 cm CFL and
weighed between 54-351 kg dressed (i.e. with the head, gill plate, and internal organs
removed). The majority of fish represented in the Yankee Co-op dataset came from
Ipswich Bay, a small area bounded to the south by Cape Anne (MA) and extending north
to the Isle of Shoals (NH). Thus, the spatial extent of sampling was restricted with
regards to the highly migratory capability of ABFT and the varied diet identified in fish
sampled throughout the Gulf of Maine (Chase 2002).

In order to expand spatial coverage, increase the numbers of observations and
acquire a more comprehensive summary of ABFT condition Gulf-wide, a second dataset
was complied from the NMFS database. This data contained 28,432 observations of
fat/oil content and shape grades from fish landed throughout the Gulf of Maine and
George’s Bank (1994 to 2007). However, this second dataset includes grades from
multiple dealers whose grading techniques varied slightly with regards to their respective
classification system (Bestor 2004). In the NMFS database assignment of grades
consisted of three levels. To examine temporal trends in fish quality, as defined
separately by fat/oil content and shape, we used multinomial logit regression with fat/oil
grade or shape grade as the dependent variable, and month and year as independent variables. The multinomial logit model estimates the probability of a fish being in grade $j$ in month $m$ and year $y$ as:

$$
\pi_j(m,y) = \frac{\exp(\eta_j(m,y))}{\sum_i \exp(\eta_i(m,y))},
$$

where $\eta_j(m,y)$ is a linear equation consisting of the variables for month ($m$) and year ($y$) and any month-year interactions. The coefficients for these variables can take on different values for each grade (McCullagh and Nelder, 1989). For example, if we treat month as a categorical variable, $\eta_j(m,y)$ can be written as:

$$
\eta_j(m,y) = \beta_{0,j} + (\beta_{1,k,j} \cdot m_k) + (\beta_{2,j} \cdot y) + (\beta_{3,k,j} \cdot m_k \cdot y)
$$

where $B_{0,j}$ is the intercept for grade $j$, $B_{1,k,j}$ is the coefficient for the effect of month $k$ on grade $j$, $m_k$ is an indicator variable denoting the month as a categorical variable, $B_{2,j}$ is the effect of year on grade $j$, and $B_{3,k,j}$ is the interaction between month $k$ and year $y$. The model for the Yankee Co-op dataset was fit using the multinomial command in the NNET library of S-PLUS V.6.2 (Insightful Corporation, Seattle, WA). The significance of each variable was tested using likelihood ratios for nested models, and Akaike’s Information Criterion (AIC) for non-nested models. The NMFS grade database was fit using the multinom command in the base package library of R version 2.8.1 (A Language and Environment for Statistical Computing, R Development Core Team, Vienna Austria).
**ABFT Condition Data**

Although large-scale commercial ABFT fishing began in 1958, detailed records regarding morphometric information (individual length and weight) were not recorded until the 1970’s. The records during the 1970’s, though extensive were not compiled and stored in central databases. Data mining for this information indicates that many of these records have been lost or misplaced prior to 1980. The first complete meristic records (i.e. individual length and weight) for commercial size (>185 cm CFL) ABFT were recorded in 1980 (note limited data exists for 1978 and 1979). The NMFS database contains individual lengths and weights of ABFT landed from 1980 to 2007 (Brad Mchale, NMFS Highly Migratory Species Division, Blackburn Drive, Gloucester MA). The original dataset contained landings information for 139,546 individual ABFT landed from the international boundary between the U.S. and Canada and along the entire east coast to the U.S. Mexican border (in the Gulf of Mexico) extending out to the 45° W international management line. This study concentrated on the feeding period from June to October along the northwest Atlantic shelf. Therefore, landings data was spatially and temporal filtered to include only those ABFT that were landed during the presumed foraging period. The NMFS management regime consists of ten discrete fishing zones that divide catch into large statistical zones (Fig 10). Landings data was filtered to remove all ABFT that were captured outside of zones 1-6 leaving only those fish captured north of Montauk, NY to the Canadian border (i.e. northern most portion of the Gulf of Maine). The selection of zones was based on documented feeding areas and historical catch records of ABFT.
Fig 10 Catch regions delineated by the National Marine Fisheries Service for commercial and recreational Atlantic bluefin tuna landings.

Over the past 28 years, the lengths of ABFT were recorded as one of the following: 1) straight fork length (defined as the straight line distance from the tip of the snout to the inner most fork of the caudal fin, 2) curved fork length (measured from the tip of the snout along the body contour above the pectoral fin and medial caudal keel to
the inner most fork in the tail) and 3) curved fin length (measured along the body contour from the anterior most insertion point of the pectoral fin to the inner most fork in the tail). In order to use all of these different types of measurements, straight fork length and curved fin length were converted to curved fork length by the following ICCAT western Atlantic conversion factors: curved fin length*1.35 and straight length/.955 (Parrack et al., 1979). The percentage of ABFT measured in each category were curved fork length 66%, curved fin length 17% and straight length 16%. Many of the straight fork length and curved fin lengths measurements were recorded prior to 1985. Thus, not utilizing these groups would have created data gaps in the beginning of the time series likely resulting in the loss of the first three years. Landings data was further filtered by removing fish captured between December 1st and May 31st and those individuals that were <185 cm CFL and >305 cm CFL. The upper and lower bounds of these size classes was based on the following; 1) lengths of 185 cm have been the legal commercial minimum size limit in the U.S for over 15 years and 2) growth studies indicate that ABFT enter a seasonal fattening cycle between 110 cm CFL and 175 cm CFL (Mather and Schuck 1960, Aguardo-Gimènez and García-García 2005). At about this size, ABFT begin to gain girth, and begin to reallocate energy from strictly growth in length into growth in weight.

Initial data exploration of the length/weight database identified significant outliers where recorded weights of fish for a particular size class were not biologically possible. For example, in 1993 a 185 cm CFL ABFT ranged in weight from 40-300 kg. In order to remove spurious data, a custom script (R version 2.8.1, the R Foundation for Statistical Computing) was written which plotted monthly weights by size class, calculated a mean
weight value, then extracted only those points which were within three standard deviations of the mean. Although filtering did not remove all potential sources of error, considerable improvement was observed in the length to weight relationship curves (Fig 11). Collectively, the filtering reduced the size of the dataframe from 139,546 to 93,914 individuals. The number of fish landed across years was highly variable (e.g., 422 in 2006 to 4059 in 1995), but each year contained a minimum of 422 individuals (Fig 5).

**ABFT Perigonadal Lipid Stores**

Atlantic bluefin tuna accumulate lipids in their muscle tissues and directly over the gonads (Fig 12) in a separate lipid store. This unique lipid storage is utilized for the production of gametes (Medina et al., 2002, Abascal et al., 2004). One hundred seventy-four adult ABFT perigonadal lipid stores were collected during two different time series, the first from 2000-2001, and the second from 2004-2007. Fish ranged from 185-324 cm CFL and samples were collected between June-October. Extracted gonads and perigonadal tissues were separated using a scalpel and individually weighed to the nearest .05 grams.
Fig 11 a-b Length to weight curves for Atlantic bluefin tuna from the NMFS database sampled in 1993 in the Gulf of Maine. a) The raw length and weight measurements. b) The length and weight measurements after the standard deviation filters were used.
ABFT Stomach Content Analysis

Though considered a generalist across its entire range, ABFT preferentially forage on Atlantic herring throughout the northwest Atlantic feeding grounds (Clay et al., 1984, Chase 2002). As a result, ABFT energy budgets rely on large volumes of high lipid prey. Therefore, substantial shifts in the diet composition or amount of consumed prey would alter the somatic condition of ABFT. The “Junkfood Hypothesis” predicts that changes in diet composition, facilitated by larger contributions of lower caloric prey can substantially alter the somatic condition of top predators. Such changes have been observed in the field for seabirds (Piatt and Anderson 1996, Golet et al., 2002) and tested
in the laboratory with pinnipeds (Rosen and Trites 2000). Within the context of this study, the junkfood hypothesis will be tested by comparing diet composition information between historic studies of ABFT stomach contents and current analysis of stomach samples collected by the Large Pelagics Research Lab. From 2004 to 2008 the stomachs of 110 adult (>185 cm CFL) ABFT were collected. Sampling occurred from June through October of each year and fish ranged in size from 185-281 cm CFL (Table 1). Whole stomachs were weighed to the nearest .05kg, contents were separated from the stomach lining, and both the stomach lining and contents were reweighed. Individual prey items were removed, identified to species (using exterior characteristic, calcified [otoliths] or chitin [squid beaks] structures), weighed and measured (total mantel length for squids, straight fork length for fish). Prey composition was calculated based on percent volume rather than prey occurrence due to the bias imposed by using % occurrence.

Table 1 Atlantic bluefin tuna stomach sampling summary.

<table>
<thead>
<tr>
<th>Year</th>
<th>June</th>
<th>July</th>
<th>Aug</th>
<th>Sept</th>
<th>Oct</th>
</tr>
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<tr>
<td>2004</td>
<td>3</td>
<td>18</td>
<td>1</td>
<td>9</td>
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<td>2005</td>
<td>4</td>
<td>4</td>
<td>8</td>
<td>13</td>
<td>1</td>
</tr>
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<td>1</td>
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<td>2008</td>
<td>9</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>

Atlantic Herring Condition Meristics Data

The NMFS Atlantic herring database from 1960-2007 contains the individual lengths and weights of over 650,000 herring. Initial exploratory analysis of this data revealed many incomplete records [where one data value (e.g. date, length, weight) was not recorded]. Removing these incomplete records yielded 462,694 individual lengths and weights. Unlike the ABFT database, the Atlantic herring length/weight records did
not have extreme outliers, and they were not filtered (Fig 13). The number of fish sampled each year ranged from 2,248 in 1960 to 25,780 in 1979. Distribution of size classes by year was highly variable owing to changes in fishing practices (i.e. near shore juvenile captured in fixed gear prior to 1988 and larger fish targeted by mobile gear) (Fig 14) and available sampling opportunities.
Fig 13 a-b Length-weight relationships for Atlantic herring sampled in Area 1A. a) Atlantic herring sampled in 1966. b) Atlantic herring sampled in 1989. No filtering was required for the length-weight database.
1996

N=6,682

1997

N=10,331

1998

N=9,104

1999

N=9,904

2000

N=9,149

2001

N=10,034
Fig 14 Length frequency distributions of Atlantic herring from the NMFS database. The number of fish and the size frequency distribution was variable across years.
Atlantic Herring Gonad and Fishing Analysis

In this study, gonads collected from Atlantic herring in Area 1A were used as proxy of population size to see if trends in gonadal weight tracked changes in population abundance. Gonad weights were obtained from the NMFS Atlantic herring database (Matt Cieri, Department of Marine Resources, Boothbay, ME). A total of 54,700 Atlantic herring gonads were collected from 1971 to 2007. Samples were not uniformly distributed across the year and representation was confined to the summer and fall months (Table 2) which includes pre and post spawning individuals.

To investigate whether there have been changes in the proportion of the TAC removed from Area 1A, commercial landings information was acquired from the Maine Department of Marine Resources (Matt Cieri, Boothbay, ME). This database contains all commercial landings from 1960 to 2007, and includes both fixed and mobile gears such as weirs, stop seines, purse seines, and trawlers. Area 1A fixed gear removals constituted the majority of landings during the early 1960’s and the early 1980’s. Since the early 1980’s, landings by mobile gear have dominated the overall TAC in Area 1A.

Foraging grounds of ABFT are located in offshore waters (Lutcavage and Kraus 1995, Chase 2002, Schick et al., 2004) thus; analysis of the temporal changes in Atlantic herring landings included only the mobile gear component of the fishery. The number of trip reports excluding fixed gear landings totaled 30,040 from 1978 to 2007. It is important to note limitations and sources of bias in this data. First, there is no information to determine the duration of each trip so catch cannot be normalized based on trip duration. Second, there is no record available to determine the changes in fishing power resulting from increased vessel horsepower, holding capacity, and net size.
However, this analysis is concerned with changes in the amount of Atlantic herring that are removed during the June to October foraging period for ABFT and whether the rate of removals tracks the changes in somatic condition of ABFT.

Table 2. Sample distribution for Atlantic herring gonads sampled and processed by the NMFS in Area 1A from 1971-2007. The remaining months contained less than 5% of the total number of samples and were excluded from this analysis.

<table>
<thead>
<tr>
<th>Month</th>
<th>June</th>
<th>July</th>
<th>Aug</th>
<th>Sept</th>
<th>Octo</th>
</tr>
</thead>
<tbody>
<tr>
<td># Samples</td>
<td>9590</td>
<td>15,673</td>
<td>19,385</td>
<td>8,142</td>
<td>1,911</td>
</tr>
</tbody>
</table>

Model Selection

Fish Condition

Fish condition is often assessed through the use of Fulton’s K or linear regression (Cone 1989). Fulton’s K, though used extensively, can present problems if K (condition) is confounded by length (Cone 1989). Linear regression confines the user to the concept of linearity and is best used to describe the overall length weight relationship across all size classes, thus it would be of little utility for capturing the variability of seasonal trends for each individual size class, particularly seasonal fattening cycles. Instead, a generalized additive model (GAM) (Hastie & Tibshirani 1990, Swartzman et al. 1992) was used to model our dependent variable (weight) as a function of three independent variables length, day of year (DOY), year and their respective interactions. In general, GAM’s are a non-parametric regression, which unlike traditional regression models is not tied to a specific relationship (linearity) while being far less restrictive regarding assumptions about the distribution of the data. GAM covariates affect the dependent variable (weight) through and additive and unspecified (non-linear, nor parametric smoothing function (Maravelias, et al., 2000) and lend themselves particularly well to
seasonal trends. One advantage of GAM’s is they allow non-linear effects of the independent variable on the response estimated from the data. Bluefin weight can be modeled as the additive sum of unspecified non-parametric smooth functions of hypothesized covariates and their interaction (Maravelias et al., 2000). A back fitting algorithm cycled through the covariates improves the smoothness at each iteration until the deviance no longer decreases (Hastie and Tibshirani 1990). With GAM analysis, the least squares estimate in the multiple linear regression is replaced with a local smoother (s or te), (Hamming 1973). The general form of the GAM is;

\[ Y = \alpha + \sum_{j=1}^{p} f_j(X_j) + \epsilon \]

where replacement of our terms yields the following equation for analyzing the condition of ABFT:

(Bluefin weight) \sim te(length) + te(year) + te(day of year) + te(length*year) + te(day of year*year) + te(length*day of year).

Assessment of Atlantic herring condition used the same model and model formula substituting in the NMFS Atlantic herring dataset as follows:

(herring weight) \sim te(length) + te(year) + te(day of year) + te(length*year) + te(day of year*year) + te(length*day of year).

**Atlantic Bluefin Tuna Perigonadal Lipid Stores and Atlantic Herring Gonad Weight**

Changes in the weight of ABFT perigonadal lipid stores and Atlantic herring gonads are seasonal in nature and like somatic condition are unlikely to express linear relationships with explanatory variables such as day of year. As such, a similar GAM
model was used to assess changes in the weight of the perigonadal lipid stores for ABFT and the gonad size of Atlantic herring. The formulas for each are as follows:

**ABFT Perigonadal Fat Pad**

\[
\text{bluefin gonad fat} \sim te(\text{weight}) + te(\text{length}) + te(\text{year}) + te(\text{day of year} \times \text{year}) + (\text{length} \times \text{day of year}).
\]

**Atlantic herring gonad**

\[
\text{herring gonad weight} \sim te(\text{length}) + te(\text{year}) + te(\text{day of year}) + te(\text{length} \times \text{year}) + (\text{day of year} \times \text{year}) + (\text{length} \times \text{day of year}).
\]

**Atlantic Herring Trip Catches**

The Atlantic herring fishery operates year round to supply markets with fresh product. Historically, landings have fluctuated throughout the year, though higher landings have traditionally been recorded in the spring and summer months. As with the previous models, relationships of landings to time of year are not linear and highly dependent on market demand and favorable weather conditions. A simple GAM model was developed to track the changes in landings as follows: 

\[
(\text{metric tons catch}) \sim s(\text{day of year}) + s(\text{year}) + s(\text{day of year} \times \text{year}).
\]

**Analysis of Catch Trends**

In the Gulf of Maine, the commercial ABFT fishery opens 1 June. Multiple regulatory measures including but not limited to monthly quotas, shipping holiday closures, and changes in minimum size have affected the temporal aspects of landings. For example, monthly quotas implemented in the early 1990’s restricted the number of ABFT landed from June to August, and in the months of September and October. Such regulatory measures were implemented to extend the fishing season which allowed equal
opportunity to fishermen in different zones and increase ex-vessels prices which typically peaked in September (Martínez-Garmendia et al., 2000). The effectiveness of monthly quotas was short-lived as the commercial fleet has not filled them before the closing dates since the middle 1990's. The inability of the commercial fleet to fill the June to August quota may be the result of the following: 1) reduced availability of ABFT to commercial fleets, 2) reduced effort or 3) changes in the arrival times of ABFT to the foraging grounds (ABFT arrive later in the season). Delayed arrival of ABFT to the foraging grounds could produce a mismatch between the peak seasonal lipid content of their preferred prey, Atlantic herring and their appearance in the Gulf of Maine.

To test this hypothesis, catch statistics were used to determine whether ABFT may have a delayed arrival time to the feeding grounds. General category (composed of rod and reel/handline gear) landings information was compiled from the National Marine Fisheries Service (Highly Migratory Species Division, Blackburn Ave, Gloucester, MA). Historically, general category landings constitute the largest sector of the Gulf of Maine fishery (quota share in the Gulf of Maine 70%) and the number of participants. This sector is least affected by weather (fish do not have to be observed on the surface) and has the largest spatial and temporal extent of any category (June 1st until quota closed, fish emigrate, or availability declines). Thus, general category landings provide the most robust estimate for monitoring fishery dependent changes compared with other gear types (e.g., purse seine or harpoon). Landings were sorted by day of year and year. Catches were tallied daily and the cumulative sum was monitored until the quota was caught, the seasons ended or there were no more catches. The final landings day was plotted against the year of occurrence and fit to a linear model. Regulatory measures (closed days,
shipping days, export holidays) imposed throughout the fishery introduce potential sources of bias in the months of September and October. To avoid these problems, another linear model was fit to landings from June 1 to August 31 each year. Limiting the data to this truncated time window normalized landings before and after 1994 when these regulatory measures were introduced.

Results

ABFT Condition Grade Analysis

The analysis conducted on the grade data from the NMFS and Yankee Fishermen's Coop identified significant declines in the somatic condition (fat and oil content and fish shape) of ABFT in the Gulf of Maine. For the Yankee Coop database fat and oil content, the effect of month, year, and the month-year interaction were each significant (all \( P < 0.0001 \)). Fish landed in the month of June arrived in poorer condition than they did in the early 1990s (Fig. 15). For example, the probability of landing a poor quality fish (grade C or worse) in June 1991 was 30% compared with 70% in 2004. Similar, but more striking results were observed in the C+ category during August and September (Fig. 15). In 1991, the probability of landing a fish in the C+ category was 16% and 9% for August and September, respectively. In 2004, that probability increased to 68% and 76% in the C+ category for August and September, respectively. Good quality fish, such as B or better currently comprise <1% of the commercial catch at this co-operative. Changes in probabilities by grade in the NMFS database followed similar patterns to the Yankee Coop data. In August and September 1994 the probabilities of being in a grade B fat grade were 61% and 74% respectively. In 2007, these probabilities dropped to 21% and 29% for those respective months (Fig 16).
The Yankee Coop data for fish shape, the effect of month, year, and the month-year interaction were each significant (all $P<0.0001$). Results for shape were similar to fat and oil content, likely because shape and fat and oil content are closely related (fat fish should have a more rotund shape). The probability of landing a fish that received a B− (lesser quality) grade for shape increased by 30%, 32%, 43%, and 28% from 1991 to 2004 for the months of July, August, September, and October, respectively (Fig. 17). For the same period, fish with a good shape (B or better) decreased by 18%, 22%, 47%, and 25% for the months of July, August, September, and October, respectively. Predicted shape grades for the NMFS database also tracked well with the trends from the Yankee Coop database. Predicted probabilities for shape grades in the B category were 75% and 81% in 1994 for August and September, respectively. Conversely, the predicted values in 2007 for the same months were 49% and 58% respectively (Fig 18).
Fig 15 The predicted probabilities of Atlantic bluefin tuna being assigned a particular grade for fat content from the Yankee Co-op database. Shifts in grades were most pronounced within the C+ category where the probabilities of being in the C+ group rose from 16% to 68% and from 9% to 75% for August and September respectively. Good quality fish comprised <1% of the catch in 2004 compared to 28% and 40% in 1991 for August and September, respectively.
Fig 16 Predicted probabilities of Atlantic bluefin tuna fat content from the multinomial model for the dealer database. Fish condition has decreased throughout the time series, particularly for late season fish. As a result, significant increases in lower fat content grades have increased.
Fig 17 The predicted probabilities of Atlantic bluefin tuna obtaining shape grades from the Yankee Co-op dataset. As with fat grades, the probability of landing an Atlantic bluefin tuna with a B shape grade has declined significantly.
Fig 18. The predicted probabilities of Atlantic bluefin tuna obtaining shape grades from the dealer dataset. As with fat grades, the probability of landing an Atlantic bluefin tuna with a B shape grade has declined significantly.
ABFT Length Weight Analysis

Overall, the final model worked well and captured 88% of the variance with the included terms. Histograms of residuals reveal values centered on zero which indicated most of the error structure is accounted for in the model (App. Fig 1.1). Plots of residuals versus fitted values by year indicate a good fit for each year in the time series (App. Fig 1.2) and no increasing scatter with increasing values. Plots of observed versus fitted values indicated very good fit between actual data points and those predicted by the model (App. Fig 1.3). This analysis identified significant changes in the somatic condition of ABFT as measured by the weight for a given length individual over the 28 year time series. All variables were considered highly significant (p<.0001) due to the extremely large number of samples in the database (Table 3). However, inferences can be made about where significant changes have occurred by observing those data points where confidence intervals do not overlap in the time series.

Table 3 Summary information for the length weight GAM model fit to the NMFS landings data for Atlantic bluefin tuna.

<table>
<thead>
<tr>
<th>Parametric Coeff</th>
<th>Estimate</th>
<th>Std Error</th>
<th>T-value</th>
<th>Pr(&gt;t)</th>
</tr>
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<tbody>
<tr>
<td>Intercept</td>
<td>5.2825548</td>
<td>0.0003998</td>
<td>13212</td>
<td>&lt;2e-16</td>
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<td>3.979</td>
<td>4.479</td>
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<td>&lt;2e-16</td>
</tr>
<tr>
<td>te(doy)</td>
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<td>4.468</td>
<td>99.91</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>te(lenyr)</td>
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<td>4.493</td>
<td>188.28</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>te(doyyr)</td>
<td>3.968</td>
<td>4.468</td>
<td>138.46</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>te(lendoy)</td>
<td>3.921</td>
<td>4.421</td>
<td>56.63</td>
<td>&lt;2e-16</td>
</tr>
</tbody>
</table>

R-sq. (adj)= 0.884
GCV score=0.015192
N=95011
Comparison between years suggests changes in somatic condition were size and temporally dependent. For example, during June, somatic condition of ABFT from 185-213 cm CFL from 1980 to 1991 declined slightly, or remained relatively stable. A significant decline was observed between 1991 and 2001, after which somatic condition began to recover. For fish 216-305 cm CFL condition over the entire time series continued to increase (Fig 19). However, in spite of an overall average increase (over the time series) for June, a significant decline was observed (from 1993-2000) where a 4 % and 2 % decline in somatic condition was observed for ABFT 208 and 267 cm CFL respectively. Similar patterns emerged for July where trends in condition were size dependent. Fish 185-198 cm CFL displayed a consistent decline in condition, whereas condition of fish 201-305 cm CFL oscillated (Fig 20). For both size classes, rapid declines in somatic condition occurred during the 1990’s. Somatic condition declined by 6% and 3% for fish 208 and 267 cm CFL, respectively. Trends in somatic condition were similar for August, September and October. Atlantic bluefin tuna 185-213 cm CFL displayed consistent declines in somatic condition throughout the time series. Fish 216-305 cm CFL had stable weights (somatic condition) during the 1980’s, experienced rapid declines during the 1990’s, then recovered condition in the early 2000’s (Fig 21).

Significant changes were also observed in seasonal lipid accumulation for ABFT in the Gulf of Maine. First, the minimum to maximum lipid accumulation and slope of the curve has decreased reducing the total amount of lipids ABFT acquired in the Gulf of Maine from June through November. Second, between 1980 and 2007, there has also been a substantial shift in the time of year when ABFT accumulate their largest lipid stores (critical window July-August). In 1980, the percentage of total seasonal lipids
accumulated during July and August was 75% for a 208 cm CFL ABFT, while in 2007 the total accumulation for that same time period was -2% (Fig 22). Total accumulation of lipids for the entire season expressed as a percentage of starting body mass was 14.8% in 1980 and 3.9% in 2007. Weights of ABFT from 2000-2005 during October were equivalent to June weights of ABFT in the 1980's further illustrating the lack of lipid accumulation across the feeding season (Fig 23). Trends in seasonal condition were similar for larger size classes of fish. The observed seasonal trends for a 267 cm ABFT are as follows: in 1980 the percentage of total seasonal lipids accumulated during July and August was 75.1% compared with 12% for 2007 (Fig 24). Total accumulation of lipids for the entire season expressed as a percentage of starting season body mass was 19% in 1980 and 7.8% in 2007. Similar to smaller fish, this size class initially lost weight upon entering the Gulf of Maine (Fig 25).
Fig 19 Predicted June weights for two size classes of Atlantic bluefin tuna. Trends in condition were size dependent, but significant declines were observed during the 1990’s. These declines represented a loss of 4% and 2% body mass for a 208 (a) and 267 (b) cm CFL Atlantic bluefin tuna, respectively. Bars indicate 95% confidence intervals.
Fig 20. Predicted July weights for two size classes of Atlantic bluefin tuna. Trends in condition were size dependent, but significant declines were observed during the 1990's. These declines represented a loss of 6% and 3% body mass for a 208 (a) cm and 267 (b) cm CFL Atlantic bluefin tuna, respectively. Bars indicate 95% confidence intervals.
Fig 21 Predicted mean weights for a 208 (a,c) cm and 267 (b,d) cm CFL Atlantic bluefin tuna in the Gulf of Maine during August (top panel) and October (bottom panel). Bars indicate 95% confidence intervals.
Fig 22 The predicted (10 day) mean weight for a 208 cm CFL Atlantic bluefin tuna for 1980 and 2007 display different patterns. Fish in 2007 enter the Gulf of Maine in poorer condition than in 1980 and lose mass before accumulating lipids at the end of the season.
Fig 23 Monthly predicted mean weights for a 208 cm CFL Atlantic bluefin tuna in the Gulf of Maine.
Fig 24 The predicted (10 day) mean weight for a 267 cm CFL Atlantic bluefin tuna in 1980 and 2007 display different seasonal patterns. Bars indicate 95% confidence intervals.
Atlantic Bluefin Tuna Perigonadal Lipid Stores Analysis

The perigonadal model explained 67.8% of the deviance and levels of significance (p<0.05) were observed for all variables (Table 4). Analysis indicated fish weight was the greatest explanatory variable determining the extent of perigonadal lipid stores. Histograms of residuals revealed values centered on zero, but the distribution did have slight tails in either direction (App. Fig 1.5). Plots of residuals versus fitted values by year indicate a good fit for each year though some error appears to be unaccounted for (App. Fig 1.6); however, no increasing scatter with increasing values is present. Plots of observed versus fitted values indicated a good fit between actual data points and those predicted by the model (App. Fig 1.7). Significant differences were observed in the weight of perigonadal lipid stores by year for each month; however, these differences
were without trend across the time series (Fig 26+27). Seasonal growth of the perigonadal lipid stores followed two distinct patterns based on the size of the ABFT. Smaller size classes (185-226 cm CFL) lipid accumulation displayed and asymptote at DOY 250 (Fig 28), while larger size classes would continue to increase the perigonadal lipid stores throughout the season (Fig 29). The seasonal growth of the perigonadal lipid stores (as a percentage of the initial value) declined over the time series. Percent increase in seasonal lipid accumulation varied by size class, for example, a 208 cm CFL ABFT increased it's perigonadal lipid stores approximately 250% over 150 days, while the increase for a 267 cm ABFT was 1,300%.

Table 4 Output from the GAM model run on the perigonadal lipid stores collected by researchers at the Large Pelagics Research Lab 2004-2008.

| Parametric Coeff | Estimate | Std Error | T Value | Pr(>|t|) |
|------------------|----------|-----------|---------|---------|
| Intercept        | -0.14013 | 0.04477   | -3.13   | 0.00207 |
| te(logwt)        |          |           |         |         |
| te(loglen)       | 2.385    | 2.885     | 12.254  | 4.34e-07|
| te(year)         | 1.000    | 1.500     | 4.761   | 0.01723 |
| te(doyyr)        | 3.724    | 4.224     | 2.933   | 0.02039 |
| te(lendov)       | 0.999    | 4.058     | 3.478   | 0.00905 |
| R-Sq.(Adj)=0.655 |          |           |         |         |
| Deviance Explained=67.8% |          |           |         |         |
| GCV Score=0.3761 |          |           |         |         |
| Scale Est=0.34876 |          |           | N=174   |         |
Figure 26 Predicted perigonadal lipid weights for a 208 cm CFL 142 kg Atlantic bluefin tuna. Significant differences were observed between years, but no trend was apparent. Bars represent the 95% confidence intervals.
Figure 27 Predicted perigonadal lipid weights for a 267 cm CFL 290 kg Atlantic bluefin tuna. Significant differences were observed between years, but no trend was apparent. Bars represent the 95% confidence intervals.
Fig 28 The seasonal predicted lipid accumulation of the perigonadal lipid stores for a 208 cm CFL 142 kg Atlantic bluefin tuna. Significant differences were observed by DOY. Black bars represent 95% confidence intervals.
Fig 29 The seasonal predicted lipid accumulation of the perigonadal lipid stores for a 267 cm CFL 290 kg Atlantic bluefin tuna. Significant differences were observed by DOY. Black bars represent 95% confidence intervals.
Atlantic Bluefin Tuna Diet

While diet studies have been conducted on ABFT (Crane 1936; Krumholtz 1959; Dragovich 1970; Mason 1976; Holiday 1978; Eggleston and Bochenek 1990), sampling does not overlap with this study and most have focused on smaller size classes. Chase (2002) sampled ABFT and most comparable size classes and geographic regions as those fish sampled in this study. Although with the Chase (2002) different sampling approaches prevent a quantitative comparison, it was possible to compare general trends in diet composition during the past 20 years. Overall, there does not appear to be a pronounced shift in the diet composition of ABFT in the Gulf of Maine (Fig 30). Diet of ABFT remains dominated by Atlantic herring with smaller contributions from other species. One notable difference was the decline of sand lance (*Ammodytes americanus*) in diet, which currently constitutes only 4% of stomach volume compared to 22% in the late 1980’s early 1990’s (Chase 2002). Though Atlantic herring still dominate ABFT diet, there was a 14% decrease by weight between the two studies. However, it should be noted that 24% of the stomach weight in the current study was not identifiable. Although a lack of intact skin or calcified structures precluded a positive identification, it is likely the unidentified portion of the diet was composed of Atlantic herring.
Fig 30 Atlantic bluefin tuna stomach content analysis (Chase 1988-1992) (LPRC 2004-2008) in the Gulf of Maine. With the exception of Ammodytes sp., there has been little change in diet composition. Note that 20% weight of stomach contents from the LPRC study were classified as unidentifiable teleosts. Although body structure resembled Atlantic herring, otoliths and skin were not available to make a positive identification.
Analysis of Catch Trends

Over the 28 year time series there is a significant difference between the final day of landings by year (Fig 31) (p<0.05). However, control measures implemented by management over the past 20 years may bias this analysis. To account for this, and normalize the catch record a second analysis was completed that only used landings from June 1 to August 31. There was a significant difference in the amount of quota landed between June 1 and August 31 by year (Fig 32) (p<0.05). The final analysis found significant differences between the DOY with the largest landings and year (Fig 33) (p=0.02). Results from the first analysis identify that the commercial fishing season for ABFT has been extended during the past 28 years. The second analysis identified that fewer fish are captured each year between June 1 and August 31 during the past 28 years. The third analysis shows the DOY with the largest landings has progressively moved later in the season during the past 28 years.
Fig 31 The final day of landings for the general category Atlantic bluefin tuna fleet in the Gulf of Maine. Last day of catch represents a filled quota or lack of availability of fish to the commercial fleet.
Figure 32 The percent of Atlantic bluefin tuna quota landed from June 1 to August 31 for the general category fleet in the Gulf of Maine.
Figure 33 The day of the year with the largest landings of Atlantic bluefin tuna by the general category in the Gulf of Maine.

Atlantic Herring Length Weight Analysis

Overall, the final model captured 98% of the variance with the included terms. Histograms of residuals revealed values centered on zero which indicate most of the error structure is accounted for in the model (App. Fig 1.8). Plots of residuals versus fitted values by year indicate a good fit for each year in the time series except for some unaccounted for error structure in years 1960, 1962 and 1968 (App. Fig 1.9) and no increasing scatter with increasing values. Plots of observed versus fitted values indicated a good fit between actual data points and those predicted by the model, with the
exception of 1960, 1962 and 1967 (App. Fig 1.10). This analysis identified significant changes in the somatic condition of Atlantic herring as measured by the weight for a given length individual over the 48 year time series. All variables were considered highly significant (p<.0001) due to large number of samples (N=462,654) in the database (Table 5). However, as with the ABFT model, inferences can be made about where significant changes have occurred by plotting and observing those data points where confidence intervals do not overlap in the time series.

Table 5 Summary information for the length weight GAM model run on the NMFS landings data for Atlantic herring.

<table>
<thead>
<tr>
<th>Parametric Coeff</th>
<th>Estimate</th>
<th>Std Error</th>
<th>T Value</th>
<th>Pr(=t)</th>
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<td>4.489</td>
<td>1474.7</td>
<td>&lt;2e-16</td>
</tr>
</tbody>
</table>

Based on the analysis of mean predicted weights for a set day of each month by year throughout the time series, changes in the somatic condition of Atlantic herring were size and temporally dependent between years. Discrete differences in the trends of somatic condition over time were observed as they related to the starting weight in the time series by the following size classes: 200-240 mm straight fork length (SFL), somatic condition trended up from 1980 to 2007, 260 mm SFL somatic condition oscillated above and below the starting weight in the time series and 280-400 mm SFL declined from the initial value (reaching the lowest levels in the late 1990's) and have recovered slightly.
For example, predicted mean weights on the first day of each month for a 200 mm SFL herring increased continuously from 1980 to 2007. These increases accounted for 9-11% of the initial body mass (1980) recorded for June through October, respectively (Fig 34). Rates were similar for Atlantic herring in the 220 mm and 240 mm SFL size classes. Predicted mean weights of herring in the 260 mm SFL size class varied by month, but in general, an average increase in weight was observed throughout the time series except October (Fig 35). Increases in body weight as a percentage of the starting weight in the time series (1980), were 0.3-3.5% for June through October, respectively. Predicted mean weights for herring between 280 mm and 400 mm SFL followed very similar patterns. For the months of June, through September weights declined from the initial data point in the time series, reached their lowest levels in the late 1990’s, then rebounded slightly. For the month of October, weights declined throughout the entire time series from 1980 to 2007. On average, weights of 320 mm SFL herring declined from their initial value in the times series (1980) by 1.85- 5.41% for June through October, respectively (Fig 36).
Fig 34 Predicted mean weights for a 200 mm SFL Atlantic herring on the first day of each month. The 95% confidence intervals are plotted but obscured by the data points in most cases.
Fig 35 Predicted mean weights for a 260 mm SFL Atlantic herring on the first day of each month. The 95% confidence intervals are plotted, but obscured by the data points.
Fig 36 Predicted mean weights for a 320 mm SFL Atlantic herring on the first day of each month. Bars indicate 95% confidence intervals.
Significant changes were observed in the seasonal lipid accumulation of Atlantic herring. Seasonal lipid accumulation curves for 200-240 mm SFL Atlantic herring increased from 1980 to 2007 (Fig 37). Throughout the time series, a 200 mm SFL herring accumulated 14.1-18.9% of its initial yearly lowest body mass over a 120 day period (Fig 37). However, like ABFT, Atlantic herring gained 69.8-70.3% of their annual weight between doy 122 and 192 over the 28 years. Lipid accumulation rates for herring in the 260 mm SFL size class decreased in the late 1980’s then increased for the remainder of the time series, exceeding the initial values in the early 1980’s (Fig 38). The 260 mm SFL herring gained 67.5% of their annual lipid accumulation between DOY 122 and 192. Seasonal lipid accumulation ranged from 17.6-22.6% of initial body weight (Fig 38). Larger herring (280-400 mm SFL) displayed different seasonal lipid accumulation cycles than smaller individuals. In general, lipid accumulation declined from 1980 to 1998, then rebounded and continued to increase until 2007 (Fig 39). For a 320 mm SFL herring, seasonal lipid accumulation accounted for 20.4-25.6% of initial body mass between DOY 72 and 192 and increased throughout the time series (Fig 39). From DOY 122 to 192 this size class gained 66 % of their total seasonal body mass.
Fig 37  a Predicted seasonal weights for a 200 mm SFL Atlantic herring for the 28 year time series with 95% confidence intervals. Seasonal weight gain increased incrementally throughout the entire time series and peaked in 2007.  b The annual seasonal weight gain for a 200 mm SFL Atlantic herring expressed as a percentage of the initial body mass. The percent increase in body mass increased steadily mirroring the increase observed in the monthly values.
Fig 38 a Predicted seasonal weights for a 260 mm SFL Atlantic herring for the 28 year time series with 95% confidence intervals. Seasonal weight gain increased throughout the time series and peaked in 2007. b The annual seasonal weight gain for a 200 mm SFL Atlantic herring expressed as a percentage of the initial body mass. The percent increase in body mass increased steadily mirroring the increase observed in the monthly values.
Fig 39  

a Predicted seasonal weights for a 320 mm SFL Atlantic herring for two separate years with 95% confidence intervals.  

b The annual seasonal weight gain for a 320 mm SFL Atlantic herring expressed as a percentage of the initial body mass. Despite declining weights during the 1990's herring were still adding the same proportion of lipids.
**Atlantic Herring Gonad Analysis**

Overall, the final model captured 69.6% of the variance with the included terms. Histograms of residuals revealed values centered on zero which indicated a large percentage of the error structure is accounted for in the model (App. Fig 1.11). Plots of residuals versus fitted values by year indicate a good fit for each year in the time series with no increasing scatter with increasing values (App. Fig 1.12). Plots of observed versus fitted values indicated a good fit between actual data points and those predicted by the model (App. Fig 1.13). This analysis identified significant changes in the yearly and seasonal gonad weight of Atlantic herring from 220-400 mm SFL (for the 37 year time series). All variables were considered highly significant (p<.0001) due to the extremely large number of samples in the database (Table 6). However, as with the ABFT and Atlantic herring length weight model, inferences can be made about where significant changes have occurred by observing those data points where confidence intervals do not overlap in the time series. The weight of Atlantic herring gonads displayed similar patterns across months. Gonad weight was lowest in 1971, peaked in 2000, then gradually declined through 2007 (Figs 40-42). The percent increase in gonad size from the minimum to maximum weight for a 220 mm SFL herring during the months of June-October ranged from 175-249%. The percent increase in gonad size from the minimum to maximum weight for a 260 mm SFL herring ranged from 53-94% from June-October. The percent increase in gonad size from the minimum to maximum weight for a 320 mm SFL herring ranged from 20-52% from June-October. Seasonal trends in gonad weight were similar across size classes. All three size classes of herring had peak gonad weights between DOY 272 and 282, coinciding with peak spawning in the Gulf of Maine.
(Sinclair and Illes 1988). However, marked differences were apparent between the size classes throughout the time series. The percent increase in gonad weight for a 220 mm SFL herring between DOY 172 and 282 increased from 274-357% from 1971 to 1998. Proportional and yearly gonad weight also increased to a peak in 1998, then declined steadily to 2007 (Fig 43). The percent increase in gonad size from DOY 152-282 for a 260 and 320 mm SFL herring followed a similar pattern increasing 419-533% and 575-738%, respectively, and continued to increase from 1971 to 2007 (Figs 44-45). Note, these gonad values are based on the mean model predicted weights of herring in each size class and will vary depending on the range of the weight parameter placed into the model.

Table 6 Model output for the Atlantic herring gonadal weight analysis.

<table>
<thead>
<tr>
<th>Parametric Coeff</th>
<th>Estimate</th>
<th>Std Error</th>
<th>T Value</th>
<th>Pr(&gt;t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>2.679841</td>
<td>0.001789</td>
<td>1498</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>EDF</td>
<td>3.835</td>
<td>4.335</td>
<td>4070.05</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>Ref.Df</td>
<td>4.335</td>
<td>3.938</td>
<td>17.60</td>
<td>2.92e-14</td>
</tr>
<tr>
<td>F</td>
<td>3.438</td>
<td>4.500</td>
<td>973.03</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>p-value</td>
<td>4.000</td>
<td>4.500</td>
<td>51.97</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>Deviance Explained=77%</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scale Est.=0.17501</td>
<td>N=54,701</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fig 40 Predicted monthly gonad weight of a 220 mm SFL Atlantic herring. Because of a data gap for 1972-1977, these estimates are model interpolations. Trends are similar across months for the time series with predicted weights peaking in 2000.
Fig 41 Predicted monthly gonad weight of a 260 mm SFL Atlantic herring. Because of a
data gap for 1972-1977, these estimates are model interpolations. Trends are similar
across months for the time series with predicted weights peaking in 2000.
Fig 42 Predicted monthly gonad weight of a 320 mm SFL Atlantic herring. Because of a data gap for 1972-1977, these estimates are model interpolations. Trends are similar across months for the time series with predicted weights peaking in 2000.
Fig 43  Predicted (10 day) mean gonadal growth for a 220 mm SFL 72g Atlantic herring. Gonad weight and proportional growth has increased significantly from 274-357% between 1971 and 1998. Overall gonad weights have declined since 1998. Bars represent 95% confidence intervals.
Fig 44 Predicted (10 day) mean gonadal growth for a 260 mm SFL 96g Atlantic herring. Gonad weight and proportional growth has increased significantly from 419-553% between 1971 and 1998. Overall gonad weights have declined since 1998. Bars represent 95% confidence intervals.
Fig 45 Predicted (10 day) mean gonadal growth for a 320 mm SFL 250g Atlantic herring. Gonad weight and proportional growth has increased significantly from 575-735% between 1971 and 1998. Overall gonad weights have declined since 1998. Bars represent 95% confidence intervals.

Atlantic Herring Landings Analysis

Over the past 47 years, there have been substantial fluctuations in landings (metric tons) of Atlantic herring by fixed and mobile gears in Area 1A during the summer foraging period for ABFT (Fig 46). Despite changes in gear types from purse seine to mid-water trawl in the 1990’s, there was little difference in trip catches between the two gears since 1994 (Fig 47). From 1960 to 1986 there were contributions from both fixed and mobile gears. However, since the middle 1980’s to present landings were
exclusively from mobile gears such as purse seine and mid-water trawlers. Analysis of Gulf of Maine herring landings from mobile gear identified significant differences in individual vessels trip catches by year and DOY (p<0.0001). Although the model converged, the low deviance explained suggests there is variability in the model not accounted for by the given main effect and interactions (Table 7). The histogram of residuals revealed values centered on zero, but skewed with a long negative tail (App. Fig 1.14). The fitted versus observed and residual versus fitted values could be improved with more variables accounting for a greater percentage of error (App. Figs 1.15, 1.16). Overall, metric tons (mt) of herring landed per trip significantly increased throughout the time series from May-October. The greatest increases in trip catches occurred in the early 1990’s, and continued through the time series (Fig 48) and this analysis identified significant differences in landings by day of year across years. From 1978-1985, the largest trip catches occurred on DOY 100. From the mid 1980’s to 1992, trip catches were relatively constant. Beginning in 1993, trip catches increased between DOY 210-310 and continued to increase throughout the time series (Fig 49). The largest difference between trip catches was observed between 1978 and 2007 (Fig 50).

Table 7 Model output from the commercial Atlantic herring landings data analysis.

<table>
<thead>
<tr>
<th>Parametric Coeff</th>
<th>Estimate</th>
<th>Std Error</th>
<th>T value</th>
<th>Pr(&gt;t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>3.580814</td>
<td>0.006026</td>
<td>594.2</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>s(doy)</td>
<td>8.975</td>
<td>9.475</td>
<td>35.83</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>s(year)</td>
<td>8.824</td>
<td>9.324</td>
<td>40.53</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>s(doyyear)</td>
<td>8.974</td>
<td>8.974</td>
<td>36.47</td>
<td>&lt;2e-26</td>
</tr>
</tbody>
</table>

R-Sq(Adj)=0.0993  Deviance Explained=10%
GCV Score=1.0918  Scale Est=1.0908  N=30,040
Fig 46 The three year moving average of herring landings for fixed (stop seines, weirs) and mobile gears (purse seine, trawlers) in Area 1A for May to Oct. Landings during the past two decades are exclusively from mobile gear fisheries.
Fig 47 Median trip catches for purse seine and mid-water trawl vessels. Both gear types recorded similar size trip catches suggesting through the time series.
Fig 48  Predicted mean Atlantic herring trip catches. Trip catches increased throughout the time series, with the greatest increase from 1995 to 2007. These catches include only purse seine, single and pair mid-water trawls.
Fig 49 Predicted mean daily trip catch from the commercial Atlantic herring fleet 1978-2007.
Fig 50 Predicted mean daily trip catches by the mobile gear Atlantic herring fleet. Significant increases in trip catches were identified across the time series.

Comparison of Atlantic Herring and Bluefin Tuna Condition

In an effort to measure the strength of association between two variables, Spearman rank correlations were performed on the following: ABFT somatic condition and Atlantic herring condition during September (208 cm CFL and 234 cm CFL ABFT vs 220, 260, 320 mm SFL herring), ABFT somatic condition and trip catches by the commercial fleet (208 and 234 cm CFL for August-October). Theses size classes of ABFT were chosen because they’re representative of commercial catches. Herring size classes were selected based on the size composition of ingested herring examined in
Correlations between somatic condition in ABFT and Atlantic herring depended on size class, i.e., some displayed either positive or negative significant correlations, or none at all (Table 8). Significant positive correlations were identified between ABFT and 320 mm SFL herring. Significant negative correlations were identified between ABFT and 220 mm SFL herring. No correlations were identified between ABFT and 260 mm SFL herring (Fig 51). Correlation analysis between the somatic condition of ABFT and the monthly mean herring trip catches (mobile gear) were all significant and negatively correlated (Tab 9). These patterns were present across all size classes during August-October (Fig 52).

Table 8 Spearman rank correlation output comparing somatic condition of Atlantic bluefin tuna with Atlantic herring and commercial landings trip catches from the mobile gear by the Atlantic herring fleet.

<table>
<thead>
<tr>
<th>Size Class Herring-Tuna</th>
<th>Null Hypothesis T/F</th>
<th>RHO Value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>220mm 208cm</td>
<td>F</td>
<td>-0.992</td>
<td>2.2e-16</td>
</tr>
<tr>
<td>260mm 208cm</td>
<td>F</td>
<td>-0.276</td>
<td>0.154</td>
</tr>
<tr>
<td>320mm 208cm</td>
<td>F</td>
<td>0.903</td>
<td>6.6e-7</td>
</tr>
<tr>
<td>220mm 234cm</td>
<td>F</td>
<td>-0.959</td>
<td>1.02e-7</td>
</tr>
<tr>
<td>260mm 234cm</td>
<td>F</td>
<td>-0.230</td>
<td>0.235</td>
</tr>
<tr>
<td>320mm 234cm</td>
<td>F</td>
<td>0.955</td>
<td>1.320e-7</td>
</tr>
</tbody>
</table>

Table 9 Spearman rank correlation output comparing somatic condition of Atlantic bluefin tuna with commercial landings trip catches from mobile gear by the Atlantic herring fleet.

<table>
<thead>
<tr>
<th>Trip Catch/Month Tuna Size Class</th>
<th>Null Hypothesis T/F</th>
<th>RHO Value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>208cm-August</td>
<td>F</td>
<td>-0.833</td>
<td>3.605e-8</td>
</tr>
<tr>
<td>208cm-September</td>
<td>F</td>
<td>-0.917</td>
<td>4.97e-7</td>
</tr>
<tr>
<td>208cm-October</td>
<td>F</td>
<td>-0.948</td>
<td>1.85e-7</td>
</tr>
<tr>
<td>234cm-August</td>
<td>F</td>
<td>-0.741</td>
<td>6.39e-6</td>
</tr>
<tr>
<td>234cm-September</td>
<td>F</td>
<td>-0.894</td>
<td>7.68e-7</td>
</tr>
<tr>
<td>234cm-October</td>
<td>F</td>
<td>-0.813</td>
<td>1.397e-7</td>
</tr>
</tbody>
</table>
Fig 51 Relationship between somatic condition of Atlantic bluefin tuna and herring in the Gulf of Maine. Bars represent 95% confidence intervals.
Fig 52 Relationship between somatic condition of Atlantic bluefin tuna and mean trip catches from the commercial herring fishery in the Gulf of Maine. Bars represent 95% confidence intervals.
The results of our ABFT somatic condition analysis utilizing qualitative grade data and morphometric measures identified highly significant changes in somatic condition of large ABFT on the temperate feeding grounds in the Gulf of Maine during the past 28 years. These changes in condition were particularly pronounced during the late summer and early fall, a period when ABFT should have reached their maximum condition factor (Rivas 1955, Butler 1974). Seasonal migrations of adult ABFT are believed to be bound by reproduction and feeding constraints: spawning in warm (>24°C) regions in spring and early summer followed by dispersal to continental shelves at higher latitudes for intensive foraging through late fall (Rivas 1955, Clay 1991). As a consequence of energetic demand from migration and reproduction, their somatic condition varies. Feeding presumably puts individuals into positive lipid balance, creating energy stores for gonadal development, metabolic maintenance and migration (Medina et al., 2002, Carruthers et al., 2005). However, throughout the past 28 years this pattern has substantially shifted. Interestingly, the initial (i.e. June) starting somatic condition of ABFT > 200cm CFL has increased throughout the time series. Despite the higher initial somatic condition entering the feeding grounds, ABFT did not attain end of season condition factors comparable to the early 1980’s, when fish had poorer somatic condition. In fact, current condition factors declined in July and early August before increasing from late August through October. This suggests that changes in the condition of ABFT are directly related to factors within the northwest Atlantic feeding grounds, and perhaps specifically in the Gulf of Maine.
Since the Gulf of Maine is a major foraging ground for ABFT, this points to potential changes in the quantity or quality of their prey as a contributing factor of somatic decline. In the Gulf of Maine, Atlantic herring are the predominant prey for adult ABFT, where depending on location, can comprise >80% of the total stomach volume by weight (Crane 1936, Chase 2002, Estrada et al., 2005). Stock assessments of age 2+ Atlantic herring in the Gulf of Maine George’s Bank complex indicate that spawning stock biomass has increased steadily from 111,600 metric tons in 1982 to a peak of 830,000 metric tons in 1997, and has since fluctuated without trend (Shepard et al., 2009). Thus, the quantity of prey would not appear to be a causal mechanism as the highest levels of abundance were calculated during the 1990’s, the time when ABFT experienced the most pronounced loss in somatic condition. However, this near historically high abundance of herring is composed of multiple spawning stocks which readily intermix, thus they are not separated for the assessment (Shepard et al., 2009). In addition, TAC’s are not uniformly distributed across the different management areas and there is a disproportionate amount of removals within the inshore component. For example, an average of 18% of the total herring stock complex resides in Area 1A, yet over the past 18 years between 48% and 90% of the annual TAC was removed exclusively from Area 1A. Such a scenario would likely reduce overall energy per unit area and increase searching times for ABFT, depressing energy budgets and potentially, could result in decreased condition. Some evidence appears to support the claim that the abundance of the entire stock complex and the inshore component may not be as high as previously estimated (Neal 2003). New assessments including updated models and catch statistics cut the total stock complex abundance in half over the past 18 years (Shepard et
al., 2009). Despite the large reduction in estimates of Atlantic herring abundance, the trend for the complex during the 1990’s was increasing, suggesting that overall, prey availability was increasing. However, gonad weights of Atlantic herring from Area 1A analyzed in this study show a steady increase through most of the time series. Increases in ovary weight of other herring stocks on the northwest Atlantic shelf have been inversely linked to population abundance, likely a result of top down density dependent control (Winters et al., 1993). Increases in ovary weight for Gulf of Maine herring were most pronounced during the mid 1990’s, indicative of a population well below carrying capacity, and in direct contradiction of projected population estimates. It is difficult to link a reduction in herring abundance to a decline in ABFT somatic condition, based solely on gonad weights as a metric. While new assessments indicate that stocks are not as robust as previously thought, the trend in abundance appears positive, and levels during the 1990’s were higher than in the 1980’s when ABFT condition was high. It is possible that the inshore component is more depleted than the remainder of the complex, but analysis of gonad weights alone is insufficient draw this conclusion, particularly since herring gonad weights are not available for these other regions.

Other than prey abundance, a decline in prey energetic quality (i.e. the caloric content per unit weight) is an alternative explanation for changes in condition of ABFT. Changes in the somatic condition of herring in the Pacific and Atlantic have been documented, and were linked to both bottom-up (climate forcing) and top-down (density dependent) effects (Schweigert et al., 2002, Engelhard and Heino 2006). Given its classification as an oceanographic transition zone (MERCINA 2001), the Gulf of Maine may be extremely sensitive to changes in climate. These climate driven changes are
partly mediated by the North Atlantic Oscillation (NAO), the dominant mode of atmospheric variability in the north Atlantic (Hurrell 1995). The NAO directly influences wind speed and direction, heat and moisture transport as well as precipitation (Hurrell et al 2003), which in turn drive oceanographic changes such as temperature, salinity, vertical mixing and circulation patterns (Visbeck et al., 2003). Phase shifts in the NAO create a "shoving match" between two dominant water masses, the Atlantic Temperate Slope Water (ATSW) and the Labrador Subarctic Slope Water (LSSW). These phase shifts have profound effects on salinity and vertical stability. Recently, modal shifts in the distribution of these water masses have been associated with phases of the NAO index (MERCINA 2001). Thus, the influence of climate on the oceanography within the Gulf of Maine/George's Bank region and subsequent impacts on fish populations is potentially extensive, particularly because this region is also a sharp transition zone for many species (Sinclair 1992). Such phase shifts can directly affect the plankton community structure (Pershing 2006, Pershing et al., 2005, MERCINA 2001), although the links are not direct in all cases and in some instances may be the results of multiple induced climate forcing effects (Rebuck and Townsend 2008). Changes in salinity and stratification in the Gulf, likely related to the export of freshwater from the Arctic, may also influence phytoplankton and zooplankton dynamics in the Gulf (Mountain 2004, Greene and Pershing, 2007, Kane 2007, Mountain and Kane 2010). Changes in physical forces affect wind fields (direction and intensity) and temperatures which, in turn, regulate thermocline depth and amount of nutrients available to phytoplankton. This determines community structure, total production and duration of the spring bloom (Drinkwater et al., 2003) and establishes the total energy available for
trophic transfer in any given year. Shifts in the composition of primary producers, for example, from diatoms to dinoflagellates (Leterne et al., 2005) can reduce food source quality available to upper trophic levels and potentially alter growth and mortality of fish (St. John et al., 2001). Some studies suggest these changes in primary producers are linked to climate through the changes in the NAO (Thomas et al., 2003). During the 1990’s, the NAO was in an extremely positive phase (Green and Pershing 2003). Changes in stratification led to more intense fall plankton blooms, particularly for smaller zooplankton species (*Psuedocalanus* sp. and *Centropages typicus*) while larger adult stages of *Calanus finmarchicus* declined (Greene and Pershing 2007). These authors hypothesize that increased autumn abundance of small copepods led to a rapid recovery of Atlantic herring. Successive years of high herring abundance led to a top down overgrazing of *C. finmarchicus*, a large contributor to dietary lipid contributions to Atlantic herring (Reid et al., 1999, Link and Almeida 2000). Abundance anomalies of *C. finmarchicus* and somatic condition of Atlantic bluefin tuna and herring display consistent trends across trophic levels (Fig 53).
Fig 53  (a) The annual abundance anomaly for *C. finmarchicus*. (b) Predicted weight of a 320 mm SFL Atlantic herring in September. (c) Predicted weight of a 267 cm CFL Atlantic bluefin tuna in September (Data from panel a Green et al., 2005).
Notably, reduction in the lipid content of individual herring would reduce per item caloric content and combined with restrictions imposed by digestive turnover rates, would limit a predator’s compensatory intake via increased consumption. Condition of herring in the Gulf of Maine has changed significantly during the same time period as ABFT, but the connection is confounded by opposing trends at different size classes. Previous and current stomach content analysis studies suggest ABFT consume Atlantic herring from 220-360 mm SFL (Chase 2002, Estrada et al., 2005, Logan et al., in prep). In this study, median Atlantic herring length sampled from ABFT stomachs between 2004-2008 was 223mm. The condition of this size herring steadily increased throughout the time series, indicating the caloric content is increasing, and therefore not responsible for the declines in condition of ABFT. Correlation analysis between the somatic condition of this size class herring and ABFT reveals a significant negative relationship. However, due to rapid digestive turnover times (Stevens and McLeese 1984) stomach content analysis (of ABFT) gives only a snapshot of diet information. This suggests that our sample size (n=102) was insufficient for capturing variability in ABFT diet. Median size of Atlantic herring captured by the commercial fleet is 260 mm SFL which reflects an abundant size class of fish available to ABFT. However, condition changes for 260 mm SFL herring are also not significantly correlated with ABFT condition. Large (>280 mm SFL) herring were identified in the bluefin tuna stomachs, but comprised only a minor portion of total herring weight. However, there were significant positive correlations between the decrease in 320 mm SFL herring condition and all size classes of ABFT. Given the complexities in herring harvesting practices, small sample size of bluefin tuna stomach contents and the lack of data on herring sizes during the period of
most rapid ABFT somatic decline, it cannot be determined that herring condition is responsible for declines in ABFT condition. Correlation between the somatic condition of ABFT and large (>280 mm SFL) herring means suggests these variables are related, however, direct cause and effect has not been established.

Similar to the effects of changes in prey quality, the composition of prey consumed can have a significant impact on somatic condition of top predators (Rosen and Trites 2000b). The “Junk Food Hypothesis” (Piatt and Anderson 1996, Merrick et al., 1997) specifically states that changes in the composition of a predator’s diet where higher caloric prey are replaced with items of lower caloric value can significantly affect the condition of several species of top predators (Kitaysky et al., 1999, Romano 2000, Rosen and Trites 2000b). The northwest Atlantic contains a variety of available prey for ABFT, all with different energetic values (Lawson et al., 1998). In the Gulf of Maine, Atlantic herring have the highest gross energy density. Atlantic bluefin tuna appear to selectively feed on high caloric prey and can optimize their energy budgets by preferentially foraging on these types of prey (Chase 2002). In theory, a reduction in herring quality/quantity could severely alter ABFT energy budgets. In previous studies, digestive efficiency, urinary efficiency and heat increment of feeding between high and low quality prey suggest that these physiological functions are substantially improved with higher quality prey (Ashwell-Erickson and Elsner 1981, Rosen and Trites 1997, Rosen and Trites 2000a). Based on current and historical stomach content analysis there does not appear to be a shift in the diet composition of ABFT (Chase 2002, Estrada et al., 2005). Given the limitation of stomach content analysis it is possible that long-term diet composition may be different, but results of stable isotope analysis for ABFT suggest that
stomach content studies accurately reflect the seasonal diet of ABFT in this region (Logan et al., submitted). Although the current analysis here does not support the junk food hypothesis, the paucity of stomach content data during the mid-1990’s, when somatic condition of ABFT was rapidly declining, does not allow this hypothesis to be rejected. For example, during the 1990’s, there may have been a concomitant increase in availability of sandlance and Atlantic herring. As an energy speculator (Brill 1996) ABFT exploit patches of highly abundant prey (Lutcavage et al., 2000). Although stomach content analysis identified herring as their preferred prey, during the middle 1990’s it is possible that ABFT targeted sandlance where large aggregations on prominent bathymetric features such as Stellwagen Bank were observed (Lutcavage et al., 2000). Having a substantially lower energy density than herring (4.4 Kg g\(^{-1}\) sandlance 9.4 Kg g\(^{-1}\) herring) (Lawson et al., 1998), increased contributions of sandlance may have reduced overall caloric intake and consequently, somatic condition. Alternatively, changes in condition may have more to do with foraging strategies and optimizing energy budgets with a large availability of high and low quality prey. For example, faced with increased abundance of two known prey species simultaneously, ABFT foraging efficiency may have declined as a result of divided foraging on both prey types as has been shown with other species (Bernays et al., 2004, Griffiths et al., 2004, Warburton and Thomson 2006). The center of distribution for ABFT in 1996 was Stellwagen Bank (Schick et al., 2004) a known hotspot for sandlance, but distributions in 1994 and 1995 were along the Maine coast, areas typically not associated with sandlance. Based on this limited amount of information, it seems unlikely that a decade decline in somatic condition could be attributed to contribution changes in the diet of ABFT.
In addition to the factors listed above, the decline in somatic condition of ABFT could be the result of changes in the composition and targeting strategies of the commercial herring fleet. Although Atlantic herring have been fished for over 400 years in the Gulf of Maine, large scale operations did not commence until the end of the 19th century (Anthony and Waring, 1980). Early fisheries were coastal and used fixed gears to capture juvenile herring. Following declines in the inshore resource, mobile gear fleets began targeting larger size classes in offshore aggregations extending to Georges Bank (Anthony and Waring, 1980). High catches resulted in rapid expansion of the fleet which precipitated a population crash in 1977 (Overholtz and Friedland 2002). Since then, population levels have continued to increase and are believed to have peaked in the late 1990’s (TRAC 2006). Although stock abundance is believed to be at high levels, in 1994 the fleet changed dramatically and switched gear from purse seine to mid-water trawlers, in order to target fresh product to supply the lobster industry (Freidland et al., 2006). These two changes have likely contributed to the significant increase in trip catches and shift in fishing, which now concentrates catches between May and October. Such changes have the potential to alter the residence time and density of prey patches. For example, larger trip catches likely result from larger sets, which may led to regional depletion of schools in specific areas. Larger sets could also reduce the residence times in localized areas. Spatial distribution of herring schools may extend over larger areas forcing ABFT to expand search patterns and energy. Some evidence suggest that schools of herring in the 1990’s may have been more dispersed across the Gulf of Maine since the search areas to catch the quota of mobile gears were three times the area than in the previous decade (Freidland et al., 2006). Thus, can ABFT assess prey patch quality
(numbers of prey/quality of prey) and could increases in trip catch size affect the foraging behavior of ABFT? There is some evidence to support this hypothesis (DeVries et al., 1989, Wildhaber et al., 1994) as some fish possess the capacity to adjust their foraging strategy as the profitability of prey patches change (Brown et al., 2006). Though ABFT are far removed from bluegill sunfish with regards to habitat and life history parameters, studies suggest the learning principles involved with foraging are very similar across taxa (Lieberman 1990). In addition to fishing pressures, environmental features affect the distribution of herring schools (Maravelias 1997, Maravelais et al., 2000), although in the Gulf of Maine these associations are not as pronounced (Friedland et al., 2006). It is difficult to assess whether a decline in somatic condition of ABFT results from changes in the commercial herring fishery since there is no data that examines how prey patch size, distribution and temporal stability of Atlantic herring schools in the Gulf of Maine have changed. Some studies have identified patch density in the Gulf of Maine, but do not distinguish these patches by species or compare across years (Gutenkunst et al., 2007). However, there are significant negative correlations between trip catches and the somatic condition of ABFT across all size classes. While it is not possible to solely attribute change in somatic condition with herring catches, there appears to be association with the somatic changes for ABFT in the Gulf of Maine. These increases in trip catches, particularly in the early part of the ABFT foraging season may have the largest impact on somatic condition.

Seasonal fattening curves from this study identified a “critical window” between July and August when Atlantic herring obtain their highest condition factor and presumably their highest caloric value. Thus ABFT should match their feeding migration
to this period in order to maximize energetic gain. Seasonal weight gain curves support this hypothesis: in the 1980’s the largest increases in ABFT mass occurred when herring reached their peak condition factor. Although Cushing’s (1982) original match/mismatch hypothesis applied to fish recruitment the association between ABFT and herring may be identical for later life history stages. Simple regression analysis indicates that the end of the fishing season (quota closing/season ending) has increased over the past two and a half decades. This could indicate that ABFT are entering the Gulf of Maine later each year, and as a consequence, miss this critical period. This analysis supports the hypothesis, though in a limited capacity. Many regulatory actions have been implemented in the ABFT commercial fishery during the past 28 years including closed days, monthly quotas and minimum size limits. All of these changes impact commercial catches and bias understanding of peak availability. It should be noted that these restrictions have been largely removed during the past 10 years, yet despite this, commercial fleets were still unable to land as many early season (June-August) ABFT. A lag between ABFT arrival times and peak herring condition could reduce acquisition of lipid reserves through a reduction in time spent on the foraging grounds, and would create a mismatch between ABFT arrival and peak herring condition. It is interesting that since the mid 1990s, mixed size classes of ABFT appeared off the Carolina coast from December to February (Block et al., 2001, Block et al., 2005), extending the range of their inshore foraging on Atlantic menhaden (*Brevoortia tyrannus*) and other species (Butler 2007). One possible explanation for the extension of the feeding season to include other inshore forage grounds could be that ABFT can no longer satisfy their energetic demands within the Gulf of Maine. The Carolina shelf waters could be serving
as a second season foraging ground to accumulate additional reserves for migration and reproduction. If the temporal or spatial aspects of migration, reproduction, and feeding patterns have changed over the past decade, alterations in the somatic and bioenergetic condition of fish feeding in the Gulf of Maine could be expected.

In pelagic fishes, migrations require a substantial energetic cost (Harden Jones, 1984), and migration distance has been linked to body size and available fat stores (Nøttestad et al., 1999). The longstanding migration paradigm is that western ABFT spawn in the Gulf of Mexico and Straits of Florida from April to June (Richards 1976; Rivas 1978; McGowan and Richards 1989) then migrate northward along the continental shelf to New England and Canadian waters (Rivas, 1955; Mather et al., 1995; Block et al., 2005, Lutcavage et al., 1999, Galuardi et al., in press, Wilson et al., 2005, Sibert et al., 2006). A substantial increase in migrants from the Eastern Atlantic may explain why the condition of fish in this region has declined. Atlantic bluefin tuna migrating to the Gulf of Maine from the eastern Atlantic would have to swim further, travel against major currents and through unproductive waters using more stored energy than individuals coming from western Atlantic spawning grounds. Significant contributions of eastern ABFT in the Gulf of Maine would miss the critical fattening window where herring obtain their presumed highest caloric value. To date, there is insufficient data to confirm that such a shift has occurred from electronic tagging (Fromentin and Powers, 2005, Lutcavage et al., 1999, Stokesbury et al., 2004, Wilson et al., 2005) and otolith chemical signatures (Rooker et al., 2006a). Another possibility is that the timing and location of spawning has shifted. The long held assumption that the New England assemblage spawns exclusively in the Gulf of Mexico and adjacent regions (Rivas, 1955; NRC 1994,
Nemerson et al., 2000, Block et al., 2005) may be incorrect (Lutcavage et al., 1999; Fromentin and Powers, 2005; Goldstein et al., 2007, Galuardi et al., in press). If fish are spawning outside of these traditional spawning grounds during May and June (Mather et al., 1995; Lutcavage et al., 1999; Wilson et al., 2005), or at different times, their somatic condition and lipid allocations would be expected to shift from historical patterns (Rajasilta, 1992). Though direct evidence of spatial and temporal changes in spawning for ABFT has not been documented and the influence of such changes (although supported by tagging results) are purely speculative at this point, reductions in lipids can severely impact reproductive potential. The relationship between food supply, energy reserves and total egg production appears tightly coupled (Mashal et al., 1999, Engelhard and Heino 2006) and loss of somatic condition can result in skipped reproduction (Rideout et al., 2005) reduced fecundity (Hislop et al., 1978) and alterations in reproductive schedules (Burton and Idler 1984, 1987, Hunter and Macewicz 1985; Larsson et al 1990; Rijnsdorp 1990; Rajisilta 1992; Rideout et al. 2000; Jorgensen et al. 2006). Calculations of reproductive output for mature East Atlantic bluefin tuna are 92.8 oocytes/g body weight (Medina et al., 2002). Constructing a basic numbers at age matrix for the West Atlantic stock and calculating the sum total of somatic loss over the time series total approximately 1,629 metric tons of biomass. Utilizing the Medina et al., (2002) fecundity estimates per gram of body weight, results in a net loss of 33 trillion eggs for the western stock, or 33 million less recruits to the fishery over the 28 year time series. Although such calculations are rudimentary they do illustrate the impact reductions in somatic condition can have on populations. Such changes in reproductive output could significantly impact estimates of rebuilding stocks to pre-1975 levels, and
create scenarios in which even the most restrictive catch controls do little to increase spawning stock biomass of ABFT.

Other possible explanations for changes in somatic and bioenergetic condition of fish include increased growth rates due to selective fishing pressure (Polacheck et al., 2004), or skipped spawning to increase growth (Jørgensen et al., 2006), but the general declines in condition in fish of such large body size are difficult to explain based on intrinsic changes in growth. This is particularly true in this study, where every fish was larger than 110 cm, the size at which the seasonal length-weight relationship begins to decrease (Mather et al., 1995) and ABFT gain more in mass than length. Declines in somatic condition could be the result of reduced foraging efficiency related to the decline in the population abundance of ABFT. It is well documented that group/school hunting facilitates better environmental sampling and provides a buffer against confusion related to schooling prey (Pitcher and Magurran 1983, Smith and Warburton 1992). Reduced abundance of ABFT on the feeding grounds could lead to reduced somatic condition through reductions in foraging efficiency. However, aerial surveys indicated substantial numbers of ABFT in the Gulf of Maine during the 1990’s (Lutcavage et al., 1997) with schools of over 5000 individuals. Thus, somatic condition appears to have declined during a time of moderate to high regional abundance of ABFT.

In conclusion, this research has identified previously undocumented significant declines in the somatic condition of ABFT and its main prey, Atlantic herring in the Gulf of Maine. The variable/s responsible for these declines have yet to be exhaustively evaluated and assigned a rank through a collective analysis, though individual analysis on each variable suggest that a synergistic bottom up and top down responses are likely.
The 1990’s, a period of rapid change in somatic condition of ABFT overlapped with large-scale changes in oceanography and middle trophic level fisheries in the Gulf of Maine. At this point it is difficult to attribute somatic declines to any one particular variable. The fact that changes in somatic condition of ABFT are occurring across the northwest Atlantic shelf suggest large scale (i.e. oceanographic or life history parameters) changes are likely responsible. However, fisheries related influences cannot be ruled out as no analysis of Canadian herring fleets has been carried out at this time. Comparative multi-trophic ecosystem models could be useful tools in evaluating what variables explain the greatest amount of variability in the data. Individual based models would be useful to examine the effects of reduced prey availability/condition on somatic condition of ABFT as well and how these changes may impact migration, reproductive potential and somatic condition (Chapman et al., in prep). The Gulf of Maine serves as an important staging ground for energy acquisition to ABFT, reductions in lipid allocations may alter migration patterns and reduce the fecundity of mature fish. Reductions in reproductive output or skipped spawning events could also severely inhibit current management efforts to increase spawning stock biomass. Furthermore, undocumented changes in the somatic condition of ABFT can further complicate setting annual TAC’s which are typically only evaluated once every four years. For example, due to the decline in somatic condition and shift to a smaller size class distribution, several thousand more fish are required to be harvested in order to fill TAC’s based on weight. Such events may partially contribute to the difficulties in rebuilding the western Atlantic ABFT population despite the inclusion of the most stringent conservation measures of any country in the Atlantic fishery and rebuilding plans which have been in place for over 15
years (ANNON 2008). A better understanding of the Gulf of Maine ecosystem and how changes in lipid flow are mediated through trophic pathways, and how energy dynamics affect migration and reproduction will facilitate better fisheries management plans with the final outcome being a stable and sustainable fishery.
CHAPTER 2

AGE AND GROWTH OF BLUEFIN TUNA IN THE WESTERN ATLANTIC

Abstract

Stock assessments for Atlantic bluefin tuna (Thunnus thynnus) in the west Atlantic utilize growth parameters estimated from direct aging or mark recapture studies that were conducted during the 1970’s. An updated growth curve for the western stock was produced by aging a total of 102 dorsal spines from Atlantic bluefin tuna (63-264 cm) landed in the Gulf of Maine between 2004-2007. A significant positive relationship (p<0.05) between fish length and maximum spine diameter coupled with direct counts of annuli and back-calculation produced a length at age key for fish 1-14 years of age. Six von Bertalanffy models were run on various combinations of the age at length key to produce final growth model parameters selected by AIC criteria. Parameter estimates for the final model $L_0$=346, $K$=0.092 and $t_0$= -0.598 are within the bounds of previous estimates, and length at age beyond age ten are significantly different (p<0.05) than the parameters currently used in the west Atlantic assessment. There was no significant difference between predicted lengths at age for the eastern and western stock (p>0.05). Estimates of K are consistent with previous studies which predict larger size at age for the western stock beyond age 5. Results suggest age and growth parameters should be updated to reflect current growth patterns for Atlantic bluefin tuna in the West Atlantic.
since small changes in growth can alter projections of spawning stock biomass and recovery plans.

Introduction

The Atlantic bluefin tuna (*Thunnus thynnus*) a highly migratory pelagic species is among the most sought after commercial fish in the world’s oceans, driven in large part by demand from developed nations (Bestor 2004). As a consequence, the Atlantic wide population is believed to be overfished (Fromentin and Powers 2005) with western Atlantic spawning stock biomass at 19% of pre 1975 levels (ANNON 2008). The International Commission for the Conservation of Atlantic Tunas (ICCAT) is granted regulatory jurisdiction for this species by signatory countries and manages the ABFT as two separate stocks. The division of eastern and western stocks is based largely on the only two known and assumed exclusive spawning areas within the Gulf of Mexico and the Mediterranean Sea (Sella 1924, 1930, Scaccini 1965, Juárez 1974b, Richards 1976, Montolio and Juárez 1977). Ancillary data supporting this division are the observations of size classes from 50 to 300 cm SFL in both management units (Bigelow and Schroeder 1953, Wilson 1965, Hamre et al., 1968, Hamre et al., 1971, Shingu et al., 1975, Tiews 1978), limited mixing across the management boundary (45° west meridian) (Brunenmeiser 1980, NRC 1994) and different size of maturity (3-5 yrs East, 8-10 yrs West) (Tiews 1963, Rodriguez-Roda 1964, Westman and Neville 1942, Turner et al., 1991, Mather et al., 1995). However, recent data suggest higher mixing rates (Miyabe and Hiramatsu 1994, Olafsdottir and Ingimundardottir 2000, Lutcavage et al., 2001, Block et al., 2005, Rooker et al., 2006a, Dickut et al., 2009) a reduced age at maturity for
western ABFT (Goldstein et al., 2007) and the possibility that growth parameters have been overestimated in the western Atlantic (Neilson and Campana 2008).

Updated assessments of age and growth parameters are critical pieces of information essential for accurate stock assessment estimation (Polacheck et al., 2004, Santamaria et al., 2008). Slight changes in growth parameters, if unaccounted for, can have profound effects on population models (Megalofonou, 2000). In particular, assumptions of constant growth rates through time (due to insufficient age and growth studies) can return skewed estimates of sustainability, stock production, and in the case of ABFT, recovery (Polecheck et al., 2004). Traditionally, direct age assessments for ABFT utilized hard or calcified structures like scales (Corson 1923a; Corson 1923b; Westman and Gilbert 1941; Mather and Schuck 1960), vertebrae (Hamre 1958; Hamre 1960; Butler 1971; Caddy and Butler 1976; Berry et al., 1977), otoliths (Caddy and Butler 1976; Nichy and Berry 1976, Hurely and lles 1983) and dorsal spines (Cort 1991; Farrungia and Rodriguez-Cabello 2001; Rosangela and Duarte-Neto 2004) to determine the age and growth parameters for ABFT populations. However, age at length keys derived from scales give inaccurate age estimates beyond six years (Mather et al., 1995), coefficient of variation with otoliths is high due to crowding of bands at the margins (Lee and Prince 1990; Mather et al., 1995) and vertebral counts vary by the sectioning techniques used (Prince et al., 1985). In contrast, dorsal spines provide more reliable counts between readers, are easy to extract, minimize damage to the fish, require minimal preparation (Rosangela and Duarte-Neto 2004), and have been used successfully in age and growth studies on ABFT and yellowfin tuna (Thunnus albacares) because they contain well

Unfortunately, age and growth parameters using dorsal spines have not been incorporated in western Atlantic stock assessment models since deposition of annuli has not been verified as an annual event (Neilson and Campana 2008) and no such studies have been conducted. Without direct age and growth data parameters, current stock assessment models utilize modal length separation for ages one to three then extract predicted values from a length age relationship (ICCAT 2003). Age slicing techniques derived from tag and recapture data (Turner and Restreop 1994) and fitted to a von Bertalanffy model provide estimates of $K$ and $L_\infty$ while $t_0$ is estimated from modal analysis (Neilson and Campana 2008). The data from the western Atlantic for the age at length estimates (Turner et al., 1991, Turner and Restrepo 1994) have assumed constant growth and are dated (approximately 90% of the mark recapture data were recorded prior to 1979). Given the fact that growth rates of southern bluefin tuna (*Thunnus maccoyii*) have changed several times over the past four decades (Polacheck) coupled with the significant changes in somatic condition (lipid stores) of ABFT along the northwest Atlantic shelf (Golet et al., 2007, Neilson et al., 2007) it is highly unlikely that growth rates have remained constant, thus an updated assessment seems warranted. This study seeks to provide updated age and growth estimates for ABFT sampled along the east coast of the United States with the goal of improving current stock assessment models that reflect the most accurate estimates of growth.
**Materials and Methods**

Atlantic bluefin tuna (n=496) were sampled over a four year period from 2004-2007 along the east coast of the United States from Virginia to the Gulf of Maine. Fish were captured by all gear types in the commercial and recreational fishery. The curved fork length (CFL) and date of capture were recorded for each fish. Curved fork lengths were converted into standard fork lengths (FL) according to the accepted ICCAT conversion factors (FL=0.955xCFL) (Parrack et al., 1979) to allow for direct comparison with other ABFT age and growth studies. The intact (including the condyle) first spiniform ray of the first dorsal fin was extracted from each fish cleaned and stored. Locations of cross sections for each spine were standardized by measuring the anterior diameter of the spine along a replacement line above the hollows, then measuring dorsally half of the measured diameter (Fig 54). A low speed Isomet saw with a diamond wayfaring blade was used to cut two serial cross sections of each spine 0.7 mm thick. Sections were washed in 70% ethanol and mounted to glass slides with Eukitt Mounting Medium (Electron Microscopy Sciences, Hatfield, PA). Sectioned spines were observed with a binocular lens microscope under transmitted light, connected to a digital camera mounted on top of the scope. Digitized images were imported and analyzed using Image J software.
Growth bands are clearly visible in the sectioned spines and can be divided into either translucent (narrow) or opaque (wide) which represent winter and summer growth, respectively. Opaque zones represent fast growth associated with summer feeding while translucent zones indicate winter growth (Cayré and Diouf 1983, Compeán-Jimenez and Bard, 1983; Cort, 1991). Marginal increment analysis indicated these translucent bands are accumulated annually (Cort 1991) and can be used as markers of annual counts. A translucent annuli and its associated opaque band were considered one year’s growth (Compeán-Jimenez and Bard, 1983; Cort, 1991; Megalofonou and De Metrio, 2000). For individuals up to three years old all of the translucent bands are visible. However, after age three the central nucleus of the spine is reabsorbed including the first annuli of life.
To overcome this, the diameter of the first visible translucent ring was measured and compared with mean values of rings from younger fish in previous studies (Cort 1991). This technique is dependent upon a strong correlation between fish length and maximum spine diameter (Compeán-Jiménez & Bard, 1983; Rey and Cort, 1984; Cort 1991, Corriero et al., 2005, Rodriguez-Marín et al., 2006). Once the age of the first translucent ring is identified, subsequent rings are counted annually to determine the age of each fish and to establish and overall age at length key. The diameters of each translucent band were measured to allow for back-calculation of length at age for each individual fish to fill in data gaps where certain length fish were not sampled. Diameter was defined and measured as the horizontal distance from outside margin to outside margin of each translucent band above the posterior notch (sulcus) where the spine curvature was reduced to its minimum (Fig 55). Proportionality between the maximum spine diameter and the length of each fish was determined by fitting a linear regression of the form $y=mx+b$ to the data. Back-calculation of lengths at previous ages was performed using the Whitney and Carlander (1956) formula for a linear relationship between body length and spine diameter. The formula is as follows;

$$L_i=-(a/b) + (L_c+a/b)(S_i/S_c)$$

where $L_i$ is the corresponding length measurements at the time when the $i$th annulus was formed, $a$ and $b$ are parameters from the linear regression between maximum spine diameter and fish length, $L_c$ is the length of fish at capture and $S_i$ and $S_c$ are the mean spine diameter for that age and spine diameter of the last annulus, respectively. Theoretical growth estimates were calculated for the raw data, all back-calculated ages, a combination of the raw data and back-calculated ages, mean ages from the raw data and
mean ages from the back-calculated data. These growth estimates were calculated by fitting a von Bertalanffy growth model (Bertalanffy von, 1938) to each of the combinations above using the Growth II software (Version 2.2.2.51 Pices Conservation Ltd Lymington, UK)

\[ L_t = L_\infty (1 - e^{-k(t-t_0)}) \]

where \( L_t \) = the predicted length at age \( t \), \( L_\infty \) = the mean asymptotic fork length, \( K \) = the growth constant (year \(^{-1}\)) (Brody coefficient), and \( t_0 \) = the theoretical age at which the fish would have been zero length. In order to compare growth estimates between studies, a growth index \( \phi \)-prime was calculated based on the formula of Pauly and Monro (1984);

\[ \phi = \log k + 2 \log FL_\infty \]

where \( k \) is the estimated growth constant and \( FL_\infty \) is the estimated asymptotic length. The potential longevity of the species was calculated using the formula from Pauly and Monro (1984);

\[ AGE_{\text{max}} = \frac{3}{k} \]

where \( k \) is the estimated growth constant. Two readings of each spine were made independently by one person. If there was disagreement between the two readings a third was conducted. If disagreement persisted, the sample was excluded.
Fig 55 Spine cross section under transmitted light. 1: maximum diameter of 1st translucent band (ending or external measurement), 2: minimum diameter of 2nd translucent band (beginning or internal measurement), 3: spine diameter.
Results

A total of 496 ABFT were sampled for this study ranging in size from 63 to 278 cm CFL. Damaged spines, and those which did not display clear translucent rings reduced the size of the data set to 102 individual fish from 63 to 264 cm CFL. Weights were not recorded for all fish in the data set and were excluded from this analysis. Based on the counts of translucent annuli lengths at age of sampled ABFT ranged from 2-14 years for the raw data and 1-14 years for back-calculated ages. Mean fork lengths were calculated for the raw data, back-calculated and the combination of raw and back-calculated ages (Table 10). Ring diameters for the sampled ABFT are given in Table 11. There was a significant positive relationship between the maximum spine diameter and the associated fish length p=<0.05 (Fig 56). Data fitted to the von Bertalanffy growth model yielded different parameter estimates, depending on the input data. The best fits were achieved by fitting the model to the yearly means for the raw data, back-calculated lengths at age and the combined raw data and back-calculated means (Table 12). All of the models were in good agreement to age 10, but the curves diverge beyond that point (Fig 57). No significant differences were observed between the predicted ages produced from the von Bertalanffy for any combination of the three data sets in Table 13 (paired t-test p>0.05), therefore the model that used the mean ages of the raw and back-calculated data was used because this model resulted in the lowest AIC value (Table 14). Estimated ages beyond the tenth year of life are significantly (p<0.05) different than the Restrepo and Turner (1994) model (Fig 58). The von Bertalanffy fits for growth curves from ABFT sampled in the east and west Atlantic using dorsal spines were not significantly different (Fig 59) (p=0.79) (Table 15). Average K values for ABFT sampled in the west
and east Atlantic across all studies was 0.097 and 0.077, respectively. Comparison of K for ABFT sampled in the west (n=1) and east (n=4) Atlantic using dorsal spines was 0.092 and 0.077, respectively. Estimated lengths at age are in agreement for ABFT sampled in the east and West Atlantic between the ages of one to four. Beginning at age five and continuing throughout the remainder of the curve, ABFT in the western Atlantic are larger on average than ABFT in the east (Table 16).

Table 10 Mean observed fork length (FL) at age of Atlantic bluefin tuna for the raw data, back-calculated age at lengths, and mean ages for a combination of raw data and back-calculated ages sampled in the eastern U.S 2004-2007.

<table>
<thead>
<tr>
<th>Estimated Age</th>
<th>Raw</th>
<th>Back-cal</th>
<th>Comb</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>73.2</td>
<td>50.06</td>
<td>50.06</td>
</tr>
<tr>
<td>2</td>
<td>104.30</td>
<td>68.15</td>
<td>68.27</td>
</tr>
<tr>
<td>3</td>
<td>119.66</td>
<td>96.49</td>
<td>96.55</td>
</tr>
<tr>
<td>4</td>
<td>154.03</td>
<td>121.30</td>
<td>121.00</td>
</tr>
<tr>
<td>5</td>
<td>177.66</td>
<td>140.23</td>
<td>140.61</td>
</tr>
<tr>
<td>6</td>
<td>184.69</td>
<td>161.12</td>
<td>162.49</td>
</tr>
<tr>
<td>7</td>
<td>189.54</td>
<td>177.01</td>
<td>176.72</td>
</tr>
<tr>
<td>8</td>
<td>208.78</td>
<td>189.76</td>
<td>187.78</td>
</tr>
<tr>
<td>9</td>
<td>217.90</td>
<td>206.71</td>
<td>204.22</td>
</tr>
<tr>
<td>10</td>
<td>219.52</td>
<td>220.44</td>
<td>215.58</td>
</tr>
<tr>
<td>11</td>
<td>232.86</td>
<td>228.85</td>
<td>222.03</td>
</tr>
<tr>
<td>12</td>
<td>242.57</td>
<td>234.04</td>
<td>231.60</td>
</tr>
<tr>
<td>13</td>
<td>264.40</td>
<td>276.00</td>
<td>264.20</td>
</tr>
</tbody>
</table>
Table 11 Mean diameter (from the outer margin of each translucent ring) of bluefin tuna \( (T. \text{thynnus}) \) spines sampled on the western Atlantic fishing grounds U.S. 2004–2007.

<table>
<thead>
<tr>
<th>Annulus</th>
<th>Radius, ( R ) (mm)</th>
<th>Min</th>
<th>Max</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td></td>
<td>2.245</td>
<td>2.896</td>
<td>2.483</td>
<td>0.1723</td>
</tr>
<tr>
<td>II</td>
<td></td>
<td>2.922</td>
<td>3.635</td>
<td>3.354</td>
<td>0.2063</td>
</tr>
<tr>
<td>III</td>
<td></td>
<td>4.349</td>
<td>5.283</td>
<td>4.801</td>
<td>0.349</td>
</tr>
<tr>
<td>IV</td>
<td></td>
<td>5.330</td>
<td>6.479</td>
<td>6.048</td>
<td>0.357</td>
</tr>
<tr>
<td>V</td>
<td></td>
<td>5.593</td>
<td>8.027</td>
<td>6.991</td>
<td>0.445</td>
</tr>
<tr>
<td>VI</td>
<td></td>
<td>6.162</td>
<td>9.062</td>
<td>7.977</td>
<td>0.487</td>
</tr>
<tr>
<td>VII</td>
<td></td>
<td>7.01</td>
<td>9.908</td>
<td>8.968</td>
<td>0.492</td>
</tr>
<tr>
<td>VIII</td>
<td></td>
<td>8.108</td>
<td>10.765</td>
<td>9.779</td>
<td>0.527</td>
</tr>
<tr>
<td>IX</td>
<td></td>
<td>9.523</td>
<td>11.605</td>
<td>10.672</td>
<td>0.512</td>
</tr>
<tr>
<td>X</td>
<td></td>
<td>10.112</td>
<td>11.844</td>
<td>11.475</td>
<td>0.546</td>
</tr>
<tr>
<td>XI</td>
<td></td>
<td>10.764</td>
<td>13.274</td>
<td>12.104</td>
<td>0.715</td>
</tr>
<tr>
<td>XII</td>
<td></td>
<td>11.540</td>
<td>14.063</td>
<td>12.750</td>
<td>0.898</td>
</tr>
<tr>
<td>XIII</td>
<td></td>
<td>12.890</td>
<td>14.639</td>
<td>13.702</td>
<td>0.765</td>
</tr>
<tr>
<td>XIV</td>
<td></td>
<td>13.922</td>
<td>13.936</td>
<td>13.929</td>
<td>0.009</td>
</tr>
</tbody>
</table>
Fig 56 Relationship between maximum spine diameter and length of Atlantic bluefin tuna sampled in the Gulf of Maine 2004-2007.

FL = 16.531x + 19.15

$R^2 = 0.9367$
Table 12 Parameter estimates derived from the von Bertalanffy growth model applied to the age and length datasets.

<table>
<thead>
<tr>
<th>Data</th>
<th>$L_\infty$</th>
<th>$K$</th>
<th>$T_0$</th>
<th>Sum Squares</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Raw Data</td>
<td>265.868</td>
<td>0.17261</td>
<td>0.100506</td>
<td>9160.64</td>
<td>936.51</td>
</tr>
<tr>
<td>Back-Cal</td>
<td>329.491</td>
<td>0.097268</td>
<td>-0.591212</td>
<td>60981.70</td>
<td>7156.9</td>
</tr>
<tr>
<td>Raw+Back</td>
<td>335.446</td>
<td>0.0971207</td>
<td>-0.546583</td>
<td>78391.50</td>
<td>8469.37</td>
</tr>
<tr>
<td>Mn Raw</td>
<td>297.211</td>
<td>0.131275</td>
<td>-0.235657</td>
<td>578.613</td>
<td>88.6683</td>
</tr>
<tr>
<td>Mn Back</td>
<td>402.392</td>
<td>0.073638</td>
<td>-0.74289</td>
<td>287.456</td>
<td>85.255</td>
</tr>
<tr>
<td>Mn RawBack</td>
<td>346.078</td>
<td>0.0922002</td>
<td>-0.598882</td>
<td>208.378</td>
<td>80.6681</td>
</tr>
</tbody>
</table>

Table 13 Predicted length at age from three datasets of Atlantic bluefin tuna sampled in the western Atlantic fishing grounds U.S. 2004-2007. The first dataset is the mean length at age for the raw data, second the mean length by age for the back-calculated and the mean lengths by age for the combination of raw data and back-calculated ages.

<table>
<thead>
<tr>
<th>Estimated Age</th>
<th>Von Bertalanffy Predicted Length</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Raw</td>
<td>Mean Back-cal*</td>
<td>Mean Raw+Backcal</td>
</tr>
<tr>
<td>1</td>
<td>-</td>
<td>48.47</td>
<td>47.44</td>
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<td>75.59</td>
<td>73.59</td>
<td>73.74</td>
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<td>126.77</td>
<td>118.62</td>
<td>119.6</td>
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<td>138.77</td>
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<td>166.12</td>
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<td>7</td>
<td>182.25</td>
<td>174.87</td>
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</tr>
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<td>8</td>
<td>196.39</td>
<td>191.02</td>
<td>189.45</td>
</tr>
<tr>
<td>9</td>
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<td>244.95</td>
<td>237.76</td>
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<td>13</td>
<td>244.91</td>
<td>256.13</td>
<td>247.30</td>
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<tr>
<td>14</td>
<td>251.35</td>
<td>266.51</td>
<td>260.00</td>
</tr>
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</table>

*Back-cal is the back calculated values based on spine diameters at previous ages.
Table 14 Comparison of von Bertalanffy growth parameters for presumed western Atlantic bluefin tuna.

<table>
<thead>
<tr>
<th>Authors</th>
<th>Year</th>
<th>Aging Method</th>
<th>FL∞</th>
<th>K</th>
<th>t₀</th>
<th>φ</th>
<th>Longevity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mather Schuck</td>
<td>1960</td>
<td>Length/Vert*</td>
<td>371.0</td>
<td>0.069</td>
<td>-1.373</td>
<td>9.15</td>
<td>43.4</td>
</tr>
<tr>
<td>Caddy et al</td>
<td>1976</td>
<td>Otoliths</td>
<td>286.6</td>
<td>0.134</td>
<td>-0.328</td>
<td>9.44</td>
<td>22.3</td>
</tr>
<tr>
<td>Butler et al</td>
<td>1977</td>
<td>Otoliths</td>
<td>277.3</td>
<td>0.116</td>
<td>-0.800</td>
<td>9.09</td>
<td>25.8</td>
</tr>
<tr>
<td>Farber/Lee</td>
<td>1981</td>
<td>Mark/Recapture</td>
<td>313.0</td>
<td>0.120</td>
<td>-0.140</td>
<td>9.37</td>
<td>25.0</td>
</tr>
<tr>
<td>Farber/Lee</td>
<td>1981</td>
<td>Vert*/Back-cal</td>
<td>401.0</td>
<td>0.080</td>
<td>-0.920</td>
<td>9.46</td>
<td>37.5</td>
</tr>
<tr>
<td>Parrack</td>
<td>1979</td>
<td>Mark/Recapture</td>
<td>313.0</td>
<td>0.090</td>
<td>-0.960</td>
<td>9.08</td>
<td>33.3</td>
</tr>
<tr>
<td>Phares</td>
<td></td>
<td></td>
<td>382.0</td>
<td>0.079</td>
<td>-0.707</td>
<td>9.35</td>
<td>37.97</td>
</tr>
<tr>
<td>Turner</td>
<td>1994</td>
<td>Mark/Recapture</td>
<td>304.0</td>
<td>0.098</td>
<td>-0.15</td>
<td>9.11</td>
<td>30.6</td>
</tr>
<tr>
<td>Restrepo</td>
<td></td>
<td></td>
<td>346.0</td>
<td>0.092</td>
<td>-0.598</td>
<td>9.30</td>
<td>32.6</td>
</tr>
<tr>
<td>Neilson</td>
<td>2008</td>
<td>Otoliths</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Campana</td>
<td></td>
<td>Dorsal Spines</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Present Study</td>
<td>2007</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Vert=Vertebrae
Table 15 The von Bertalanffy predicted length at age from dorsal spines for Atlantic bluefin tuna from the current study and mean length at age from the east Atlantic.

<table>
<thead>
<tr>
<th>Age</th>
<th>Estimated Fork Length at Age (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Current Study</td>
</tr>
<tr>
<td>1</td>
<td>47.30</td>
</tr>
<tr>
<td>2</td>
<td>73.55</td>
</tr>
<tr>
<td>3</td>
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<td>7</td>
<td>174.01</td>
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<td>14</td>
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<tr>
<td>15</td>
<td>263.61</td>
</tr>
<tr>
<td>16</td>
<td>270.85</td>
</tr>
<tr>
<td>17</td>
<td>277.45</td>
</tr>
<tr>
<td>18</td>
<td>283.48</td>
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<tr>
<td>19</td>
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<td>293.99</td>
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<td>323.27</td>
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<td>30</td>
<td>325.27</td>
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</table>
Table 16 The mean length at age estimates across all studies for Atlantic bluefin tuna sampled in the eastern and western Atlantic.

<table>
<thead>
<tr>
<th>Age</th>
<th>Mean Fork Length (cm)</th>
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<tr>
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<td>1</td>
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<td>317.02</td>
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<td>30</td>
<td>319.67</td>
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Fig 57 Fitted growth parameters to the different length at age datasets. The growth curves are in good agreement until 10 years of age, when divergence occurs.
Fig 58 von Bertalanffy estimated lengths at age for four age and growth studies of Atlantic bluefin tuna in the western Atlantic utilizing otoliths, dorsal spines, vertebrae and mark recapture.
Discussion

An up to date estimation of growth parameters for ABFT derived from von Bertalanffy models has not been conducted in the west Atlantic since 1994 (Turner and Restrepo 1994). This last age and growth assessment is based upon data collected in the early and mid-1970’s. This study provides the most current information on the relationship between maximum spine diameter and fork length, the mean length at age for
the sampled and back-calculated populations, the von Bertalanffy growth parameter estimations and comparisons with previous studies in the west and east Atlantic. This study confirmed the relationship between maximum spine diameter and fork length which is important for back-calculation where the relationship between hard parts (otoliths, fin rays) and animal size will grow in a predictable relationship (Smith 1983). The presence of this relationship in the current study provides for a more robust estimation of size at previous ages for age classes not well represented by the original data, and confirms the utility of such calculations as has been demonstrated in other tuna species (González-Garcés and Fariña-Perez 1983, Rosangela and Duarte-Neto 2004). The similar estimations of length at age from the raw data and the mean back-calculated lengths at age derived from the von Bertalanffy model reinforce this relationship.

In this study, ages of ABFT were calculated for individuals from 1-14 years. Readings of spines from older individuals was complicated by the lack of clarity and crowding of rings at the margins, problems encountered in previous studies (Lee et al., 1983), where individuals larger >270 cm SFL were not represented in the original database. The estimated von Bertalanffy growth parameters for this study produced an asymptotic length of 346 cm fork length and a Brody growth coefficient of 0.092. These values are well within the bounds estimated from previous growth studies in the western Atlantic (Table 5). The longevity and growth index values are also within the upper and lower bounds of previous studies (Table 5). The growth curves estimated in the current study follow similar estimates derived by Turner and Restrepo (1994) rather than those estimated by Neilson and Campana (2008) and Parrack and Phares (1979) (Fig E). Despite the lack of significant differences in the predicted lengths at age between the
current study and the Turner and Restrepo (1994) there is an apparent divergence of predicted length at age beginning at age 10 that becomes significant from 10 to 30 years. Differences in the curves between these two studies could result from the different methodologies used to estimate the growth parameters. Turner and Restrepo (1994) used mark and recapture data whereas the current study used dorsal spines. Cross comparisons between studies that utilize different age techniques could confound the interpretation of these results. The von Bertalanffy estimates from this study are in close agreement with growth parameters estimated in the eastern Atlantic using dorsal spines (Fig G). This is a strong argument for consistent methodologies across studies which minimize introduced error and allow for direct comparisons. It is clear that grouped growth estimates (otoliths, vertebrae, spines, mark and recapture) from the western Atlantic display different growth parameters (Table 5) and these differences may be a direct result of the methodologies used. Various methodologies have been implemented to age fish including size frequency analysis, mark and recapture and counting of annuli on hard parts (Campana 2001). Despite the latter being the most utilized (Santamaria et al., 2008) there are potential errors associated with ring adsorption, interpretation of multiple marks close together and lack of knowledge regarding the age of released fish (Compeán-Jimenez and Bard, 1983; Cort 1991, Turner and Restrepo 1994, Santamaria et al., 2008). This unaccounted variability may be the basis for the observed differences in the growth curves.

Conversely, differences between the curves could be the result of changing trophic feeding patterns manifested over the past three decades. Thirty years separate the Turner and Restrepo (1994) growth estimates and those of the current study and in that
time the northwest Atlantic shelf has experienced significant changes (Frank et al., 2005, Green and Pershing 2007). Changes in the somatic condition of ABFT along the northwest Atlantic indicate that energy acquisition on the feeding grounds has shifted in large (i.e., >176 cm SFL) ABFT (Golet et al., 2007, Neilson et al., 2007). Energy acquisition is the major determinant of fish growth (Brett and Groves 1979) so a reduction in intake during the summer foraging period would affect growth rate. However, the extent of this has not been quantified. Fishing pressure can alter growth strategies of tuna stocks (Polacheck et al., 2004), but fishing pressure in the western Atlantic has remained stable relative to stock size for the past two decades (ANNON 2008). Previous studies all demonstrated that, in general, ABFT in the western Atlantic have a larger $L_\infty$ and lower $K$ which results in a larger length at age beyond five years. The current study is no exception, and even when compared against other studies in the eastern Atlantic which used dorsal spines, these estimates are still higher for the western Atlantic. This trend has been supported by multiple age and growth studies utilizing various methodologies, suggesting that the observed differences are the response of the stocks themselves rather than an artifact of methodologies. Several hypotheses may explain these differences, but age of maturity and fishing pressure are the most plausible. The onset of maturity shifts energy allocation from somatic to gonadal growth (Medina et al., 2002) and high fishing pressure can reduce the age of maturity (Polacheck et al., 2004). Estimated ages of maturity are 8-10 years in the western (Turner et al. 1991, Nemerson et al. 2000) and 3-5 years in the eastern Atlantic (Rodriguez-Roda 1964, Susca et al., 2000, 2001b, Medina et al., 2002, Corriero et., 2005), although this difference has been questioned (Goldstein et al., 2007). Shifts in energy allocation from growth to
reproduction at ages three to five for eastern ABFT would presumably slow overall somatic growth which has been observed in the calcified structures of other teleosts (Campana 2001). This maturity schedule matches the time period where a divergence occurs with length at age between ABFT sampled in the eastern and western Atlantic. Fishing pressure is known to decrease mean body size and age and increase growth rates which can shorten the time to maturity (Torsen 1986, 1990, Rijnsdorp and Leeuwen 1996). Fishing pressures in the Mediterranean have likely exceeded recommended TAC’s during the previous decades (ANON 2003, 2007, 2008) and may have contributed to the divergence in length at age between western and eastern Atlantic growth studies.

Fin rays have been used successfully in previous age and growth studies (Compeán-Jimenez and Bard 1983, Cort 1991, Farrugia and Rodriguez-Cabello 2001, El-Kebir et al. 2002, and Rodríguez-Marín et al. 2004), and one of these (Cort 1991) serves as the baseline for assessment of the eastern Atlantic stock, but these studies have been confined to the eastern Atlantic. The current study is the first of its kind to use identical structures for ABFT sampled in the western Atlantic. Such methods have potential drawbacks such as the adsorption of the nucleus including rings from the first years of life and multiple depositions of hyaline rings in the same year, both observed in this study. Sampled fish are assumed to be from the western stock, but mixing of eastern and western origin fish occurs annually (Block et al., 2001, 2005, Rooker et al., 2006a, Dickut et al., 2009, Galuardi et al., in press) and can complicate interpretation of growth parameters.

However, the establishment of mean ring diameters for thousands of fish during the first year of life appears to validate the use of spines for aging studies. Second, there
have been no validation studies utilizing tagging and injection of oxytetracycline. Such experiments are often expensive and reliable returns are unlikely to be realized. However, the deposition of annual rings has been validated with marginal increment analysis in the west and east Atlantic (Faber and Lee 1981, Megalofonou and De Metrio 2000). The deposition of multiple rings within a single year from changes in migration patterns (Compeán-Jimenez and Bard, 1983) or diet (Cort 1991) may increase variability between readings, but such observations have been well documented and are easily discernable. Dorsal spines have proven to be an effective tool for aging highly valued fish such as ABFT. This is because their extraction is quick, causes little to no damage to the fish’s appearance (i.e., market price reduction) and their rings are highly visible. However, as suggest by others (Rooker et al., 2007, Santamaria et al., 2008) it is advisable that future studies integrate multiple approaches (length based modeling, hard parts, tag and recapture) into a single growth model (Eveson et al., 2004) which can be used to identify the differences observed between age and growth parameter estimates from the eastern and western Atlantic. This study provides an updated growth curve for the western Atlantic, which due to common methodologies employed by current eastern Atlantic studies will allow for direct comparison of growth rates between fish sampled in each region. Future work should be directed at obtaining a more robust sample of individuals across a wider length distribution, establishing a separate western Atlantic mean ring diameter key, collecting and aging multiple structures from the same individual, validating stock origin (chemical signatures) and if possible validate ages by incorporating conventional, electronic and chemical tagging.
CHAPTER 3

DISTRIBUTION OF ATLANTIC BLUEFIN TUNA IN THE GULF OF MAINE

Abstract

Declines in commercial landings of Atlantic bluefin tuna have occurred in the Gulf of Maine from 2004 through the 2009 fishing season. Because migratory patterns of Atlantic bluefin tuna are complex, declines in landings in one region cannot be assumed to represent a reduction in spawning stock biomass. Although the distribution of bluefin schools in the Gulf of Maine was partially linked to their proximity to SST fronts, their relationship to preferred prey may be stronger. This study fit generalized linear and additive models to fishery dependent landings data collected from fishermen’s logbooks for Atlantic bluefin tuna (1979-2005) and from vessels trip catch reports for Atlantic herring in the Gulf of Maine in order to examine shifts in distribution. Interactions of four main effects (Day of Year* Year, Latitude*Day of Year, Latitude*Year and Longitude*Year) were significant (p<0.05) in explaining surface distribution of Atlantic bluefin tuna in the Gulf of Maine. Mean longitude of Atlantic bluefin tuna schools shifted east > 350 kilometers in 26 years (-71.33 to -68.08°W). Latitude of Atlantic bluefin tuna schools ranged from 42.72-40.95°N without trend. Latitude of Atlantic herring landings ranged from 42.323-44.191°N and longitude of Atlantic herring landings ranged -70.189 to -67.915°W. Distances between Atlantic bluefin tuna surface schools and the 95th percentile utilization distribution of herring densities were significantly
Atlantic bluefin tuna (Thunnus thynnus) occupy different oceanographic regions throughout the Atlantic and exhibit a wide thermal range (4-30°C) (Rivas 1955, Mather et al., 1995, Lutcavage et al., 1999, Block et al., 2001, 2005, Wilson et al., 2005). Large size (Bigelow and Schroeder, 1953), endothermic capacity (Carey and Teal 1966, 1969; Carey et al., 1971, Carey and Lawson 1973) and elevated metabolism (Brill 1996) confer the largest horizontal and vertical range of all the tuna species. These adaptations allow ABFT to exploit highly productive (O'Reilly and Busch 1984) temperate water masses along the continental shelf that contain large aggregations of high energy prey such as Atlantic herring and mackerel (Lawson et al., 1998, Sinclair and Iles 1985). This provides ABFT with two distinct advantages over tropical tuna species, namely, 1) profitability of prey capture is higher (energy per unit volume) along the shelf regions (Lawson et al., 1998) and 2) the predictability of prey patches along the shelf region appears more stable (Friedland et al., 2006) than sub-tropical and tropical environments (Blackburn 1968). This allows ABFT to maximize foraging budgets and accumulate substantial intra-musculature lipid stores (Rivas 1954, Butler 1974; Golet et al., 2007) between years. Consistent and highly profitable foraging (i.e. high lipid accumulation
Atlantic bluefin tuna have been observed in this region since the turn of the 20th century (Crane 1936, Caddy and Butler 1976, Lutcavage and Kraus 1995, Mather et al., 1995, Lutcavage et al., 1997, Ortiz et al., 1999, Brown et al., 1999, Brown 2007).

Distributions of tuna species are nonrandom (Sibert and Fournier 1994, Sibert et al., 1996, 1999) often exhibiting highly clumped aggregations because spatial distributions are connected to specific environmental features necessary for reproductive and foraging success (Cushing 1982, Sinclair Iles 1985, MacCall 1990, Mann 1993). Distributions of tunas across ocean basins are regulated by broad scale environmental features (Nakamura 1965, 1969, Mendelson and Roy 1986, Lehodey et al., 1997). Requirements for successful larval development aggregates ABFT into high salinity regions above 24°C for short periods (Richards 1976; Mather et al., 1995), but thermal stress (NRC 1994, Blank et al., 2004) coupled with the energetic demands of spawning induce a northward migration to temperate water masses. This suggests that at the most basic level, ABFT movements and temperature regimes are likely related over the broad scale (Humston et al., 2000), and that individuals seek to attain and maintain positive somatic energy stores by selecting appropriate environments (Chapman et al., in prep). Tuna distributions over large scales are linked to specific environmental features (Nakamura, 1969; Sund et al., 1981; Laurs et al., 1984) and in some cases catch has been linked to sea surface temperature (SST) and chlorophyll (Laurs et al., 1984; Fiedler and Bernard, 1987). Understanding what conditions structure distributions of tunas at smaller scales (e.g., The Gulf of Maine) is complicated because potentially complex biophysical
variables determine intra and inter-annual distributions (Maury et al., 2001, Royer et al., 2004, Schick et al., 2004).

In the Gulf of Maine, surface schools of ABFT are highly clumped, and often confined to discrete regions (Lutcavage and Kraus 1995, Lutcavage et al., 1997). Distributions change annually and are associated with SST and distance to frontal zones (Schick et al., 2004). Ultrasonic telemetry (Lutcavage et al., 2000; Brill et al., 2002, Gutenkunst et al., 2007), modeling (Humston et al., 2000; Newlands and Lutcavage, 2001), pop-up satellite tagging (Lutcavage et al., 1999, Stokesbury et al., 2004, Block et al., 2001;2005, Wilson et al., 2005, Sibert et al., 2006), environmental analyses (Schick et al., 2004, Schick and Lutcavage 2009) and aerial surveys (Lutcavage et al., 1997) have been used to track ABFT distributions in the Gulf of Maine. Due to limited, real time information on distribution, efforts to link these distributions with environmental or biological variables have been constrained to short periods (i.e., one week) (Schick and Lutcavage 2009) or small numbers of fish schools examined (Gutenkunst et al., 2007). Information on the changes in distribution of pelagic, highly migratory fishes is needed since CPUE data alone may not adequately represent stock abundance (Hilborn and Walters 1992; Quinn and Deriso, 1999; Mesnil et al. 2009)). Landings of ABFT in the Gulf of Maine (2005-2009) are approximately 30% of the annual TAC (ANNON 2008). Currently, assessment models for ABFT rely heavily upon fishery dependent data (CPUE). Ten of eleven indices used in current assessments are fishery dependent (Polacheck et al., 1998, ANNON 2008) Catch per unit effort can be biased based on fishing areas utilized by the fleets, markets (Bestor 2004), effort controls, and by shifts in distribution of fish. For example, in the Gulf of Maine, shifts of 300 kilometers can make
ABFT unavailable to 95% of the U.S. fleet (most of the U.S. fleet fishes within 200 km of shore), which are primarily day boats, and would place the center of distribution across international boundaries (e.g., George's Bank). From 2004-2009 the commercial ABFT fishery in the Gulf of Maine (purse seine, general and harpoon categories) failed to catch its allocated quota (Neilson et al., 2007). As a result, northern U.S. CPUE has declined (ANNON 2008) and western Atlantic TAC's have been lowered in the event that a reduced level of U.S. catch is a direct result of reduced abundance of the western stock(s). It has not been investigated whether the declines in the U.S. CPUE are the result of reduced availability of ABFT due to shifting distributions, and what factors may account for these shifts. The objectives of this study are 1) to characterize the surface distributions of ABFT from 1979 to 2005 in the Gulf of Maine, 2) to examine the spatial distributions of Atlantic herring catches from 1996 to 2007 in the same region, and 3) to determine whether ABFT schools are associated with areas of high herring density.

Materials and Methods

Atlantic Bluefin Tuna Dataset

Spatially explicit information on the distribution/landings of ABFT in the Gulf of Maine is temporally and spatially limited. The NMFS collects landings information, but fish are assigned to large statistical areas (1000's kilometers) inadequate to discern changes in distribution on smaller scales (10's to 100's kilometers) (Fig 9). Fishery linked aerial surveys of ABFT (Lutcavage et al., 1997) limited to a few years of documentation (1993-1996, see Lutcavage and Kraus 1995) provided real-time, high resolution positions of
surface schools in the Gulf of Maine. However, no time series of ABFT distribution greater than three years exists for the commercial fishery in the Gulf of Maine.

Fishery dependent data from 1979-2005 was collected from logbooks maintained by captains of commercial fishing vessels (purse seine and harpoon) to create a time series of high resolution landings information for ABFT. Purse seine vessels and harpoon boats typically utilize spotter pilots to locate ABFT schools comprised of fish meeting minimum landing size for that category. Purse seine vessels generally target surface schools containing tens to hundreds of individuals, and generally return to port to offload when the hold is filled or target number of fish has been landed. In contrast, harpoon boats target individual fish until the day’s bag limit is reached or conditions are no longer suitable. Therefore the amount of search conducted by the vessel and vessel’s pilot varies with fishing category. In each case, the spotter pilot shares information with the vessel crew regarding the surface distribution and sizes of observed schools, as well as estimate of sizes of individuals comprising the school. Purse seining and harpoon methods are similar in that they are each surface fisheries that require relatively calm seas and good visibility, and thus share some aspects of search effort and fishing conditions.

Vessel captains generally recorded detailed descriptions of each school observed including the time of day, date, location (latitude and longitude or Loran C), and (usually) number of fish observed in the school or captured by the vessel. Data from these logs was transcribed into digital format and where applicable, Loran C (time distance) locations were converted to latitude and longitude. All Loran C positions were transformed into latitude and longitude using the Loran GPS Pro software (Arden Software Co. Indialantic, FL). This software utilized the Additional Secondary Factors (ASF)
correction tables which provided the most accurate conversion between the two coordinate systems, by accounting for the fact that Loran signal propagation over land distorts the signal and can delay the arrival time of the wave by an average of five microseconds. This conversion provides an accuracy of 0.2 microseconds or 100ft.

The final dataset of logbook information contained 671 individual schools (>two individual fish) with a total of 46,350 individual fish observed or captured from 1979-2005. Distribution of these observations was not uniform across the entire time series with most schools observed in August and September (Fig 60). These data are obviously fishery dependent and positions of schools are biased by fishermen behavior and search and fishing objectives of the captain and crew (including spotter plane). Landings data only provide information on where fish are based on the location and search area of vessels and spotter plane. They do not account for areas not surveyed by the fleet and cannot be used to interpret the presence or absence of fish on other regions in the Gulf of Maine. However, based on presumed economic interests of the captain and crew, it is assumed that fishermen will fish in regions where catch is profitable and adjust their fishing effort to changes in fish distribution as well as quality. This study tracked the historic to current distribution of surface schools observed by fishermen. The study assumes that fishermen will minimize costs by fishing in regions closest to shore and expand effort to offshore areas as needed. Thus, logbook observations are well suited to examine the onshore offshore location of landings over the extent of the fleet’s range in the Gulf of Maine.
Fig 60 Yearly observations for the number of schools and total number of fish observed each year. Note scales are not identical due to variability in observations each year.
Atlantic Herring Dataset

Commercial landings of Atlantic herring have been recorded and archived by the Maine Department of Marine Resources since 1960. These records tally several variables including but not limited to: date, catch weight (mt), gear type, and location. There are several caveats with this dataset which need to be addressed. First, catch locations are divided into two time periods based on spatial resolution. From 1960 to 1995 catches are aggregated and recorded in 10 minute squares regardless of gear type, which (similar to the NMFS ABFT tuna database) are of limited utility for describing fine scale changes in distribution. In 1996, commercial herring vessels were required to maintain vessel monitoring systems (VMS) that recorded the position of each vessel’s trip landings. This provided a 12 year time series of herring catches in the Gulf of Maine. Second, there have been several modifications of gear type and upgrades in vessel capacity and horsepower that cannot be directly accounted for here. From 1960-1985, landings alternated between fixed (weirs, stop seines) and mobile gear (trawlers, purse seine) fisheries (Fig 61). Since 1985, commercial catches have been almost exclusively from mobile gears (mid-water trawls and purse seine vessels) which target herring outside state waters (>three miles). There is insufficient ancillary data to accurately account for the changes in gear, effort and vessel modification which have occurred. However, the extent of these changes can be minimized by selecting portions of the time series with the highest catch resolution, similarity in vessels, gear type and TAC allocation. To do this, the database was filtered to include trip catches from 1996-2007 (years where VMS was used), purse seine and trawl gear (combined account for >95% of landings), and fishing zones 1A, 2 and 3 where there is overlap between ABFT foraging grounds and the
Atlantic herring fishery. The final database yielded 15,062 positions suitable for analysis.

Fig 61 Atlantic herring landings from the inshore (Area 1A) Gulf of Maine commercial fishery. Post 1985, landings have been exclusively from mobile gears.
Model Selection for Distribution Changes

Given the dynamic nature of the marine environment and prior knowledge of historical Atlantic herring and bluefin tuna distributions (based on historical fishing patterns), it is unlikely that distributions and time have a linear relationship. For this reason, a generalized additive model was used to examine the changes in distribution of herring and ABFT. Complete details of this model and rationale for its application here are presented in Material and Methods of Chapter 1. For ABFT and Atlantic herring, a full model was run which included all main effects and their respective interactions. The final models are as follows:

Bluefin Tuna Observation Model

\[(\text{lognumbers} \sim s(\text{year}) + s(\text{doy}) + s(\text{lat}) + s(\text{long}) + s(\text{doyyear}) + s(\text{latlong}) + s(\text{latdoy}) + s(\text{longdoy}) + s(\text{latyear}) + s(\text{longyear}))\]

Atlantic Herring Commercial Catch Model

\[(\text{logmt}) \sim (\text{doy}) + (\text{year}) + (\text{lat}) + (\text{long}) + (\text{doyyr}) + (\text{latlong}) + (\text{longdoy}) + (\text{yearlat}) + (\text{yearlong})\]

Kernel density Estimation for Grid Interpolation

In an effort to 1) identify the spatial distribution of ABFT and Atlantic herring across the Gulf of Maine, and 2) create an interpolated surface density and avoid common problems associated with traditional histogram analysis (width of the bins and end points of the bins), non-parametric density estimators were used to visualize how the spatial distribution of Atlantic herring and bluefin tuna have changed. Specifically, a two-dimensional kernel density estimation with an axis-aligned bi-variate normal kernel,
evaluated on a customized 500 by 500 square grid was used. The boundaries of the grids were defined based on the complete spatial distribution of catches and all areas where fishery dependent data could have been collected. The ABFT grid was bounded from 40°N to 45°N and -71°W to -66°W, while the Atlantic herring kernel grids were 39°N to 45°N and -71°W to -65°W. Kernels were created using the kde2d function within the MASS library in the statistical package R. Kernels were weighted according to the number of ABFT observed or captured (for the ABFT tuna dataset) and by the metric tons of catch on an individual trip basis for Atlantic herring. The most common form of density estimation is:

\[ \hat{f}(x) = \frac{1}{nb} \sum_{j=1}^{n} K \left( \frac{x - x_j}{b} \right) \]

where \( x_1, \ldots, x_n \) are the samples, \( K \) is a fixed kernel (\( \cdot \)) with a bandwidth \( b \) (Venables and Ripley 2002). Optimal bandwidth was determined using the bandwidth.nrd function located in the MASS library in the statistical package R, a well supported rule for finding the optimal bandwidth (Venables and Ripley 2002). This function determines the optimal bandwidth through the following function:

\[
\{ \\
\text{r} <- \text{quantile(x, c(0.25, 0.75))} \\
\text{h} <- (\text{r}[2] - \text{r}[1])/1.34 \\
\text{4} * \text{1.06} * \text{min} (\text{sqrt} (\text{var(x)}), \text{h}) * \text{length(x)}^{\text{-1}/5} \\
\} \text{ where r utilizes the 25th and 75th utilization distributions for optimal bandwidth selection. For the ABFT database, kernels were computed on a yearly and monthly time}
\]
step to examine intra and inter-annual changes. Kernels for the Atlantic herring database were computed on a monthly and two week time step.

**Bluefin Tuna and Atlantic Herring Spatial Relationships**

To examine the spatial relationship between herring and ABFT schools (i.e., whether tuna schools are located closer to Atlantic herring schools than schools distributed at random), a customized script was created in R. This script measured the straight line distance between schools of ABFT and Atlantic herring and the randomly generated schools of ABFT in the Gulf of Maine. To do this quantile and contour commands were used to identify three different utilization distribution values (50\(^{th}\), 75\(^{th}\) and 95\(^{th}\) percentile) which surrounded each kernel produced on a monthly and two week time period from the Atlantic herring commercial catch data (Fig 62). Atlantic herring and bluefin tuna are highly mobile species, and capturing the spatial relationship between their co-locations is highly dependent on the time step picked for the analysis. Each species is capable of moving 40-80 kilometers over 24 hours, and spatial distributions are subject to higher variability with longer time periods. Given the nature of fishery dependent data the selected time period has to balance reducing the time step to a sufficiently small window to capture distributional patterns while retaining enough catch positions to provide reliable estimates of distributions. Thus, kernel densities computed at monthly time steps could underestimate the spatial dispersion by aggregating catches which displayed uneven sampling. For example, large catches in a two week period combined with moderate catches in other regions during a different two week period would bias the kernels towards the larger catches for the first two weeks and underestimate the densities in the following two weeks.
Fig 62 Kernel density estimations from Atlantic herring commercial landings calculated over a one month time step. The black borders surrounding the density estimations represent the 50\textsuperscript{th} (a) 75\textsuperscript{th} (b) and 95\textsuperscript{th} (c) percentile utilization distribution values.
Examination of kernel densities calculated on a monthly and two week time interval appear to support this claim (Fig 63). After visually examining kernel density contours at each of the three percentiles (50, 75, and 95) the 95th percentile was chosen as the most appropriate. This is the most conservative value with regards to the area enclosed by the different contour lines and provided the most rigorous test for identifying whether or not there is a spatial relationship between Atlantic herring and bluefin tuna. For example, in August 2003, the 50th percentile results in five high density areas, the 75th percentile includes three, while the 95th percentile encloses only one (Fig 64). Thus, choice of a specific utilization distribution has the potential to substantially alter the outcome of this analysis by allowing several more possible areas of high herring density with lower utilization distribution values. Though the 95th percentile is the most conservative value, given the mobility of ABFT and Atlantic herring, it seems to be the most appropriate for preserving the potential spatial bias involved with producing kernel estimations over longer time periods, and for including all but the densest aggregations of Atlantic herring. Furthermore, significance at the highest utilization distribution would preclude testing of additional utilization distribution values. Next, for each two week time interval, the actual kernel density values for the 95th percentile contour were identified. The two week kernel grids and their corresponding 95th percentile utilization distribution values were imported into a custom R script which: 1) used the utilization values to identify the borders of each kernel at the 95th percentile boundary for each two week interval, 2) calculated a surface distance (accounting for spatial curvature) between all of the 95th percentile values bounding each kernel and each ABFT location for that two week period (using the Geo-dist function within the GMT library in R), and 3) used a minimum
distance function which retained only a single value corresponding to the shortest distance between any given ABFT location and the associated herring 95th percentile utilization distribution. The second part of the script utilized the same functions, but calculated distances from randomly generated points within the grid to the closest 95th percentile utilization distributions of the herring catches. A 2:1 ratio was used as a guide to the number of randomly generated points selected during each time interval. A Gulf of Maine bathymetry grid was used to limit the spatial distribution of randomly selected points by using a depth limit that removed the possibility of random points being selected on land or in areas within the Gulf of Maine where ABFT are not found (i.e., estuaries, rivers etc). Finally, a generalized linear model was used to compare the distances calculated between the 95th percentile utilization distribution of Atlantic herring schools, ABFT surface schools and randomly generated school locations using the following: glm(dist~type), where dist is a continuous variable containing all the distances calculated from both the ABFT and randomly selected points and type is a categorical variable which assigns the type of corresponding distance (e.g. tuna or random).
Fig 63 Kernel density estimations of commercial Atlantic herring landings divided into two week (a+b) and one month periods (c). Smoothing over a one month time step (c) can mask the changes in distribution over shorter periods (a).
Fig 64 Kernel density estimations of commercial Atlantic herring landings and the contour lines at the 50\(^{th}\) (a), 75\(^{th}\) (b) and 95\(^{th}\) (c) percentile utilization distribution values for the first two weeks in August 2003. Each utilization distribution produced different enclosed areas of high kernel density.

Results

Bluefin Tuna Distribution

The GAM model showed significant differences in the distribution of ABFT with the given independent variables. Interactions of four main effects (Day of Year* Year, Latitude*Day of Year, Latitude*Year and Longitude*Year) were significant (p<0.05) in
explaining surface distribution of Atlantic bluefin tuna in the Gulf of Maine (Table 17). The model converged, but only explained 22.7% of the deviance (Table 17). A histogram of residuals was centered on zero, but had long tails (Fig 1.17). Residual versus fitted and observed versus fitted values could be improved with the inclusion of additional explanatory variables (Appendix Fig 1.18 +1.19). Mean longitude of Atlantic bluefin tuna schools continued to move east > 350 kilometers in 26 years (-71.33 to -68.08°W) (Fig 65). Latitude of Atlantic bluefin tuna schools ranged 42.72 to 40.95°N without trend (Fig 65). Yearly kernel density estimations exhibit broad distribution patterns of ABFT over the time series (Fig 66). Distributions of ABFT during June (1992-2005) have been stable without any continuous trend. Changes in latitude were less than one degree while longitude varied by 0.6 degrees between years (Fig 67). These values represent a small number of schools, thus caution should be applied to the interpretation of these results (Fig 59). Distributions of ABFT in July were more variable than June with a min-max range of 1.79 and 1.76 degrees for latitude and longitude, respectively (Fig 68). Latitude and longitude did not display long-term directional trends. Variability in distribution of ABFT was greatest in August with a min-max difference of 2.35 and 3.67 degrees for latitude and longitude, respectively (Fig 69+70). There were no directional trends observed for latitude. For longitude, mean position of schools shifted to the east for the entire period by > 350 kilometers. The min-max changes in mean school position for September were 2.09 and 2.62 for latitude and longitude, respectively (Fig 71). Latitude did not show long-term directional shifts, but from 1990-2002 schools shifted from the northern to southern Gulf of Maine. The yearly mean longitude position exhibited a consistent shift eastward. In 2005, a single school of 30
fish shifted onshore, but obviously, this single data point is insufficient to detect any
trend. The min-max changes in latitude and longitude for October were 1.3 and 1.9
degrees, respectively (72). No continuous trends in school distribution were observed for
latitude or longitude.

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<th>Std Error</th>
<th>T Value</th>
<th>Pr(&gt;t)</th>
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<td>1.765</td>
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<td>1.4125</td>
<td>1.913</td>
<td>4.404</td>
<td>0.01382</td>
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</table>

| R-Sq (Adj)=0.19 | Deviance Explained=22.7% |
| GCV Score=1.4474 | Scale Est=1.3782 | N=657 |
Fig 65 (a+b) The yearly mean positions of Atlantic bluefin tuna schools in the Gulf of Maine. Changes in latitude (a) oscillate between 41 and 43 degrees with no directional trend. Longitude (b) positions display a consistent easterly movement across the time series.
Fig 66 Kernel density estimations (left) and the positions (right) of Atlantic bluefin tuna in the Gulf of Maine.
Fig 67 The mean latitude (a) and longitude (b) of Atlantic bluefin tuna observations/catches in the Gulf of Maine for June. Error bars indicate standard deviations. Observations for June did not start until 1992.
Fig 68 The mean latitude (a) and longitude (b) of Atlantic bluefin tuna observations/catches in the Gulf of Maine for July. Error bars indicate standard deviations. Continuous records were not recorded until 1992.
Fig 69 The mean latitude (a) and longitude (b) of Atlantic bluefin tuna observations/catches in the Gulf of Maine for August. Error bars indicate standard deviations.
Figure 70 Kernel density estimations for the catches/observations of Atlantic bluefin tuna in the Gulf of Maine during August. Plots show easterly shifts in distribution throughout the time series.
Fig 71 The mean latitude (a) and longitude (b) of Atlantic bluefin tuna observations/catches in the Gulf of Maine for September. Error bars indicate standard deviations. Note, 2005 includes only one school of 30 fish observed inside Cape Cod Bay, MA.
Fig 72 The mean latitude (a) and longitude (b) of Atlantic bluefin tuna observations/catches in the Gulf of Maine for October. Error bars indicate standard deviations.
Atlantic Herring Distributions

Overall, the GAM model fit to the commercial Atlantic herring landings database captured 9% of the deviance. All variables except Latitude*DOY were significant. A considerable portion of this significance is due to the large sample size (n>15,000). The effect of year and the DOY*Year and Year*Latitude interactions had the highest significance (Table 18). Model checking revealed a highly skewed histogram of residuals with a large negative tail (Appendix Fig 1.20), poor fits for the observed versus fitted and residual versus fitted values (Appendix Fig 1.21+1.22). In the current form, the model lacks sufficient explanatory power to predict spatial distributions of Atlantic herring with a high degree of confidence. However, model data was used to examine densities of catch relative to latitude and longitude by year and month using kernel density estimates and bubble plots. Mean position of landings was stable, did not display continuous directional trends, but contained a high degree of variability throughout the time series (Fig 73). Monthly mean latitude and longitude positions of catch by month were also stable, shifting a maximum of 1.8 and 1.5 degrees within any one month, respectively (Table C) (Figs 74+75). High densities of Atlantic herring were variable across months, and unlike ABFT, did not exhibit long-term directional trends (Figs 76-81). Based on the mean monthly kernel density estimates, the relationship between the location of landings and year varied by month. For latitude, high density catches were consistent between 43-44°N in May and June (82). High densities continued to be landed between 43-44°N during July and August, and extended south between 41-42°N (Fig 82). Catches dispersed over a broad area in September, but became concentrated between 42.6 and 43.5°N during October (Fig 83). For longitude analysis, catches were distributed
over broad areas (>2 degrees) from May-September (Figs 84+85). Two distinct areas of catch developed at 70.4 °W and 67.8°W in September and high density catches become more concentrated at 70°W in October (Fig 85).

Table 18 Summary of the GAM model fit to the Atlantic herring landings database.

| Parametric Coeff | Estimate | Std Error | T Value | Pr(>|t|) |
|------------------|----------|-----------|---------|----------|
| Intercept        | -1.900e-2| 3.363e-3  | -5.649  | 1.64e-8  |

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<td>2.81e-15</td>
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<td>s(yearlong)</td>
<td>3.138e-04</td>
<td>7.888e-05</td>
<td>3.978</td>
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R-Sq(Adj)=0.0893  Deviance Explained=8.98%
GCV Score=1.4706  Scale est=1.4697  N=15,062

Table 19 Maximum and minimum distribution values of commercial herring landings in the Gulf of Maine.

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Figure 73 The mean latitude (a) and longitude (b) for landings by the commercial herring fleet in the Gulf of Maine. Error bars represent standard deviations.
Fig 74 Mean latitude for landings from the commercial Atlantic herring fleet in the Gulf of Maine. Error bars represent standard deviations.
Figure 75 Mean longitude of landings from the commercial Atlantic herring fleet in the Gulf of Maine. Error bars represent standard deviations.
Fig 76 Estimated kernel densities of commercial Atlantic herring landings in the Gulf of Maine.
Fig 77 Estimated kernel densities of commercial Atlantic herring landings in the Gulf of Maine.
Fig 78 Estimated kernel densities of commercial Atlantic herring landings in the Gulf of Maine.
Fig 79 Estimated kernel densities of commercial Atlantic herring landings in the Gulf of Maine.
Fig 80 Estimated kernel densities of commercial Atlantic herring landings in the Gulf of Maine.
Fig 81  Estimated kernel densities of commercial Atlantic herring landings in the Gulf of Maine.
Fig 82 Mean positions of kernel density estimates from commercial Atlantic herring landings. Diameter of each point is proportional to the size of the catch (mt).
Fig 83 Mean positions of kernel density estimates from commercial Atlantic herring landings. Diameter of each point is proportional to the size of the catch (mt).
Fig 84 Mean positions of kernel density estimates from commercial Atlantic herring landings. Diameter of each point is proportional to the size of the catch (mt).
Atlantic Bluefin Tuna and Atlantic Herring Spatial Relationship

Highly significant differences were observed between distances calculated from the 95th percentile utilization distributions of Atlantic herring densities, position of ABFT surface schools and the randomly generated ABFT surface schools (p<2e-16) (Table 20). Based on this analysis, the distance between schools of ABFT and high densities of Atlantic herring is not random. Results identified schools of ABFT located closer to high densities of Atlantic herring than points at random. This suggests that concentrations of Atlantic herring may be one of the principle drivers of ABFT distribution in the Gulf of Maine. Out of one hundred two week time periods between June 1 and October 31, ABFT were observed within the 95th percentile utilization distribution of Atlantic herring 17 times (Fig 86). The remainder of ABFT schools were located either inside or along the margin of the 50th percentile utilization (Fig 87), or not associated with high density areas of herring (Fig 88).
Table 20 The GLM output from the distances between Atlantic bluefin tuna schools, randomly generated points and the 95\textsuperscript{th} percentile utilization distribution of herring densities.

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Fig 86 Kernel density estimations of Atlantic herring landings with some Atlantic bluefin
tuna schools (solid black points) located within the 95th percentile utilization distribution.
Fig 87 The kernel density estimations of Atlantic herring landings with Atlantic bluefin tuna schools (solid black points) located within or along the margin of the 50th percentile utilization distribution.
Fig 88 The kernel density estimations of Atlantic herring with Atlantic bluefin tuna schools (solid black points) not associated with high densities of Atlantic herring landings.
Discussion

A comprehensive understanding of the physical and biological drivers underlying the spatial distributions of large pelagics is a key component to improving fisheries management. This can provide a predictive framework with which to test specific hypotheses regarding shifts in distribution and how those shifts relate to changes in CPUE. Complicating such analyses is the collection of data on similar time and spatial scales (Schick et al., 2004). This study provides the framework for future spatial modeling by identifying shifts in the distribution of ABFT and herring in the Gulf of Maine and synthesizing multiyear datasets with high resolution landings information.

The GAM model fit to the fishery dependent observations of ABFT did not account for a large degree of variance. Given the current main effects and their interactions, shifts in distribution of ABFT are significant. During August and September ABFT schools moved progressively east centering their distribution on George’s Bank. At the same time, landings of ABFT in the Gulf of Maine declined while CPUE in adjacent regions (southwest Nova Scotia, U.S. and Japanese longline fleet) was stable or increased (ANNON2008, McAllister et al., 2008). Two hypotheses: 1) reduced availability of ABFT in U.S. waters, and 2) range contraction as a result of reduced western Atlantic spawning stock biomass have been proposed for these changes (McAllister et al., 2008). Overfishing and shifts in prey distribution are also explored in the current study.

Atlantic bluefin tuna fisheries are subject to high variability (Nakamura 1965, Tiews 1978, Pusineri et al., 2002, Takeuchi et al., 2009) as a result of complex migration patterns of the species (Lutcavage et al., 1999, Block et al., 2001, Block et al., 2005,
Wilson et al., 2005, Sibert et al., 2006; Galuardi et al. in press). Two examples were the Nordic purse seine and Japanese longline fisheries which began and ended within 15 years. Retrospective analyses suggested overfishing and lack of recruitment (increasing size classes over time) were mechanism to explain the decline in this fishery (Nottestad 2009). Decline in the Brazilian fishery was linked to the meta-population concept where the assemblage went extinct or joined adjacent groups (Takeuchi et al., 2009) which adapted different migratory pathways and did not succumb to overexploitation (Fromentin and Powers 2005).

From 1994 to 2004, mean size of ABFT increased by 35 cm CFL in the Gulf of Maine (Fig 4). However, unlike the Nordic fishery, CPUE analysis have identified two strong year classes that will recruit to the commercial fishery (Brown 2007, 2009) provided they return to the Gulf of Maine. Thus, recruitment is still occurring in the Gulf of Maine. Large size classes of ABFT have been landed in southwest Nova Scotia and the Gulf of St. Lawrence (Neilson et al., 2007) during the same time that Gulf of Maine landings have declined (2005-2009), although there is a slight increasing trend since 2008 (NMFS ANON?). The presence of these large, presumably mature size classes in Canadian waters does not support the length based migration hypothesis either (Nøttestad et al., 1999). Strict quotas since 1981, stable fishing mortality (ANNON 2008), increasing CPUE in adjacent fisheries (Neilson et al., 2007), and no decline in the larval survey (McAllister et al., 2008) [although this time series has serious limitations] do not support the hypothesis that the Gulf of Maine ABFT assemblage was fished out.

This study documented a shift in distribution of ABFT schools in the Gulf of Maine ~350 kilometers to the east. The shift has taken place during a period (August and
September) of high seasonal abundance (Lutcavage and Kraus 1995, Lutcavage). It is important to note that 15-30% of the annual quota from 2005-2009 was captured in the Gulf of Maine, which indicates that some fish > 185 cm FL (the minimum size for commercial landing) are still utilizing this area, and availability of juveniles and presumably adolescents has increased (Brown 2007, 2009). Large-scale environmental changes have been linked to declines in landings over broad geographic regions (Marsac 1999; Ravier and Fromentin 2004), and the shift from mainly schools of adults to mainly schools of juveniles here also suggests that additional factors are at play. Additional studies have focused on correlating surface school distribution of ABFT with environmental variables (Humston et al. 2001, Royer et al., 2004, Schick et al., 2004). Schick et al., (2004) and Royer et al., (2004) examined the relationship between surface school distribution of ABFT and environmental variables (SST, fronts, chlorophyll) in the Gulf of Maine and Gulf of Lion, respectively. In these studies, the majority of spatial structure associated with schools was unaccounted for by the given variables. Both authors stressed the importance of incorporating prey data into the models. Schick and Lutcavage (2009) extended this analysis by including prey data which improved the model. However, this analysis relied upon interpolated prey densities extracted from trawl surveys limited to a one week period. Prey distribution was the most significant variable in the model, but extension of the conclusion to longer time periods (i.e., months, years) was not possible.

Stomach content analysis (Chase 2002) and stable isotope data (Estrada et al., 2005, Logan et al., submitted) have identified Atlantic herring as the most important prey item for ABFT in the Gulf of Maine. This study identified significant differences in the
distances between schools of Atlantic herring and ABFT. These results compliment the findings of Schick and Lutcavage (2009) by expanding the time series across the entire foraging season (June-October) for ten years. This suggests that ABFT schools are associated with high densities of Atlantic herring and could explain the spatial structure not accounted for in the original Schick et al (2004) and Royer et al (2004) studies. Furthermore, these results confirm the importance of including prey data in future models to describe changes in ABFT distribution on the foraging grounds. However, despite strong spatial connectivity between these two species it did not appear that changes in the distribution of ABFT can be entirely explained by shifts in herring distribution. Changes in temperature, vertical mixing and wind fields affect the formation and stability of fronts and bottom temperatures, known aggregating mechanisms for herring (Murawski 1993, Maravelias 1997). So although the distribution of ABFT may not be directly linked to the environment per se, environmental conditions will determine the locations of herring aggregations which will influence ABFT.

In this study, the mean distribution of Atlantic herring varied by month and year. Location of landings in May, June and July were relatively stable, and showed no clear signs of directional trend in either latitude or longitude. Landings in August and September had higher variability and in some instances coincided with distribution shifts of ABFT surface schools. Movements of Atlantic herring are related to temperature (Murawski 1993, Maravelias and Reid 1997, Corten 2001), diet preferences (Sherman and Honey 1971, Sherman and Perkins 1971), primary productivity (Maravelias and Reid 1997, Corten 2001), and fronts (Friedland et al., 2006), variables which are non-linear and dynamic (Maravelias et al., 2000). Given that, it is interesting that catch latitudes in
May, June and July are stable from year to year, although this stability has been identified in other parts of the Atlantic (Maravelias et al., 2000). While the mean distribution of Atlantic herring and bluefin tuna did not always overlap, the GLM analysis and kernel densities identified schools of ABFT that were significantly associated with regions of high herring density. Prey patches are more abundant than predators and gradient search patterns (Friedland 2006) will aggregate ABFT in select regions where profitability is high (Marschall et al., 1989, DeVries et al., 1989). It is impossible for ABFT to simultaneously exploit all available prey patches, so it not surprising results from this study showed many areas of high herring density without ABFT. However, schools of ABFT are associated with high herring densities and the overall shifts in distribution followed the broader pattern of exploitation and rebuilding for Atlantic herring stocks in the Gulf of Maine.

In the Gulf of Maine, abundance of herring stocks has varied by region (e.g., inshore Gulf of Maine, Nantucket Shoals, George’s Bank). After declines in the late 1970’s, in 1984, abundance of the inshore Gulf of Maine Atlantic herring stock increased (Overholtz and Friedland 2002). Abundance increased throughout Nantucket Shoals in 1987 and on George’s Bank in 1992 (Overholtz and Friedland 2002). Shifts in distribution of ABFT follow this pattern as larger observations/catches moved from the inshore Gulf of Maine to the Great South Channel and then George’s Bank. Conditions along the northwest Atlantic shelf have been favorable for ABFT foraging over the past 15-20 years (Lawson et al., 1998, Frank et al., 2005, Shepard et al., 2009), yet despite high densities of Atlantic herring in the western Gulf of Maine from 2004-2007 (Overholtz and Friedland 2002, TRAC 2006), landings of commercial size ABFT remain
low, although with a slight upward trend since 2008. These same conditions exist off the Norwegian coast (Nøttestad et al., 2009) and ABFT have yet to return. Previous Atlantic herring stock assessments estimated spawning stock biomass at 1.4 million metric tons (TRAC 2006), but recent assessments reduced that by 50%. Though the inshore component of the herring stock comprises only 18% of the total stock complex (Shepard et al., 2009), it has routinely provided 60% of the total TAC, potentially depleting the inshore component. Successive years of poor foraging could force ABFT to adjacent foraging grounds as profitability declines. This transmission of social learning in fishes is well established in the literature (Pitcher and House 1987, Ryer and Olla 1991, 1992) where patch choice is determined and then reinforced with positive feedback similar to the “win stay lose leave hypothesis” (Randall and Zentall 1997).

Significant atmospheric and oceanographic changes occurred in the Gulf of Maine during the previous two decades (Greene and Pershing 2007) and the potential effects these changes have had on zooplankton communities and groundfish recruitment (Pershing et al., 2005, Pershing 2006) are well documented (Drinkwater 2002), but there is no information on how these changes may impact distributions of ABFT. Chapter One outlined the significant change in somatic condition of Atlantic herring, and bluefin tuna which appears to have coincided with significant changes in the composition of the zooplankton community (Pershing et al., 2005, Pershing 2006). Changes to the bottom-up propagation of lipids is worthy of future investigations as it will affect prey patch quality. Although several species of fish have the capacity to assess patch quality (Marschall et al., 1989, DeVries et al., 1989), it is not possible to determine if ABFT are capable of doing so or whether or not there is significant changes in lipid transfer
between years. New results from life history modeling suggest that ABFT need to, at a minimum, maintain energy stores in order to spawn annually (Chapman et al., in prep), and thus, over a long lifespan, should seek forage grounds and migration paths with the highest energetic returns.

Although caution should be applied with regards to the comprehensiveness of the models describing spatial changes in distribution of Atlantic herring and bluefin tuna and there is a need to include better explanatory variables, some conclusions can be drawn from this analysis. First, an eastward shift in mean longitude of ABFT schools in August and September is evident and likely to persist in light of additional independent variables added to the model, which may help to explain a greater degree of the variance. Second, directional movement of Atlantic herring is not as consistent as ABFT in latitude or longitude, and may be confounded by the interaction of management policies and market demands. Finally, these analyses have confirmed that locations of ABFT are found closer to high densities of Atlantic herring than schools distributed at random. Consistent with Royer et al (2004) and Schick et al (2004) who found that inclusion of prey in future models would provide a more robust framework and add to the predictive power of spatial models. Now that comprehensive data sets have been compiled for both ABFT and Atlantic herring, the next step is to build a spatially explicit model which incorporates fishery dependent data (i.e., catches) and additional variables including SST, frontal density, chlorophyll, bathymetry and possibly others. Such models, provided they contain temporally appropriate and high resolution data, may help resolve the spatial relationships between the large pelagic predators like ABFT and its prey, as observed with other species (Polovina 1996, Jaquet and Gendon 2002, Benoit-Bird and Au 2003).
Integration of fishery dependent data into modeling frameworks has the potential to provide fisheries managers with additional resources to maintain the sustainability of pelagic fish stocks around the world.
CONCLUSION

Significant declines in the somatic condition of ABFT have been identified in adult size classes in the Gulf of Maine during the past two decades. The reason(s) for these declines cannot be attributed to a single factor, but changes to the somatic condition of Atlantic herring, the trip catches for the commercial Atlantic herring fleet and reductions to the inshore 1A abundance of Atlantic herring may collectively be contributing to these declines. Thus, a reduction in ABFT lipid stores may be a result of both top down and bottom up processes acting simultaneously. Significant changes in growth parameters past age ten have also been identified for ABFT sampled in this study. It is not possible to attribute the changes in growth to the decline in lipids at this time. Significant changes in the spatial distribution of ABFT have been identified with schools moving to the east throughout the time series. Schools of ABFT are significantly associated with schools of herring in the Gulf of Maine and may be the principle variable explaining inter-annual shifts in distribution. Collectively, these changes indicate conditions in the Gulf of Maine may no longer sustain the energetic demands of ABFT. Documenting shifts in distribution and somatic condition of highly migratory species will improve assessments models which explicitly account for changes in numbers at age and reproductive output and further the understanding of what drives complex migration patterns in ABFT.
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APPENDIX

Fig 1.1 Histogram of residual values and frequency of occurrence. The error structure of the model seems to be well accounted for as the majority of points are centered around zero and follow a normal distribution.
Fig 1.2 Yearly plots of fitted versus residual values. The model fits each year well with most points centered on or near zero with minimal scatter and no apparent trend with increasing values.
Fig 1.3 Yearly plots of observed versus fitted values for the Atlantic bluefin tuna length weight model. Tight clustering of points throughout the data series indicate good model prediction based on available observations. The model fits each year well with minimal scatter from minimum to maximum values.
Fig 1.5 Histogram of residual values and frequency of occurrence. Considerable error is accounted for in the model, though the distribution contains tails and is off center of zero.
Fig 1.6 Residual versus fitted values for the Atlantic bluefin tuna perigonadal lipid storage model.
Fig 1.7 Observed versus fitted values for the ABFT perigonadal lipid storage model.
Fig 1.8 Histogram of residual values and frequency of occurrence for the Atlantic herring length weight database. The error structure of the model is well accounted for as the majority of points are centered around zero and follow a normal distribution.
Fig 1.9 Residual versus fitted values for the Atlantic herring length weight model. Most years provide a good fit, but there is some scatter in the relationship in years 1960, 1962 and 1968.
Fig 1.10 Observed versus fitted values for the length weight Atlantic herring model. All years provide good measures of fit with the exception of years 1960 and 1962.
Fig 1.11 Histogram of the frequency for the residuals in the Atlantic herring gonad model. The error structure of the model is well accounted for with points centered on zero and following a normal distribution.
Fig 1.12 Residual versus fitted values for the Atlantic herring gonad model. Note, there was no data for the years 1972-1977, therefore those years are not included in the figure.
Fig 1.13 Yearly plots of fitted versus observed values from the Atlantic herring gonad model.
Fig 1.14 Frequency of residuals from the Atlantic herring catch database.
Fig 1.15 The Atlantic herring trip catch analysis model fitted versus residual values.
Fig 1.16 The Atlantic herring trip catch analysis model fitted versus observed values.
Fig 1.17 Frequency of residuals from the Atlantic bluefin tuna landings database.
Fig 1.18 Plots of residual versus fitted values for the GAM model on the Atlantic bluefin tuna landings data.
Fig 1.19 Plots of observed versus fitted values for the GAM model on the Atlantic bluefin tuna landings data.
Fig 1.20 Frequency of residuals from the Atlantic herring catch database.
Fig 1.21 Residual versus fitted values from the GAM model fit to the commercial Atlantic herring landings database.
Fig 1.22 Observed versus fitted values from the GAM model fit to the commercial Atlantic herring landings database.