

Life History and Stock Structure of Atlantic Bluefin Tuna (*Thunnus thynnus*)

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*Our understanding of the biology of Atlantic bluefin tuna (*Thunnus thynnus*) has increased profoundly in the last decade, and the progress is attributed to the development and application of a variety of novel tools. Here we provide a comprehensive examination of available data on the life history and stock structure of *T. thynnus* by re-examining current databases and literature and highlighting findings from recent studies using approaches such as archival tags and natural markers (e.g., genetics, otolith chemistry). The present review provides a detailed synthesis on the reproductive biology, feeding ecology, growth, mortality, migration, and stock structure of *T. thynnus*. In addition to characterizing key life history attributes and discussing stock-specific (east versus west) differences, the implication of trans-Atlantic movement and mixing are addressed. We also identify significant data needs that still exist and must be addressed to promote effective management and rapid recovery of *T. thynnus* populations.*

Keywords Atlantic bluefin tuna, migration, reproduction, growth, mortality, feeding, stock structure, management, archival tags, genetics

1. Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) is the largest member of the family Scombridae (mackerels and tunas) and often regarded as a quintessential predator of pelagic ecosystems. *Thunnus thynnus* possess derived evolutionary traits, both physiological and morphological,

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allowing them to effectively exploit a wide range of pelagic environments from warm tropical to subpolar waters of the North Atlantic Ocean (Mather et al., 1995; Collette, 2001; Fromentin and Powers, 2005). Similar to their Pacific congener (*T. orientalis*) (Bayliff et al., 1991; Bayliff, 1994), *T. thynnus* display highly migratory behaviors and trans-oceanic movement is well documented (Mather et al., 1995; Turner and Powers, 1995; Block et al., 2005; Rooker et al., 2006a). Large-scale movements between foraging and spawning grounds often result in *T. thynnus* crossing international management boundaries. Thus, coordinated international cooperation is critical to effective management of *T. thynnus*, and the success of these efforts is dependent upon improving our present understanding of their life history and stock structure (Porch, 2005).

Current management of *T. thynnus* is based on the premise of two principal zones of spawning and juvenile production, occurring in the Mediterranean Sea and Gulf of Mexico. Although trans-Atlantic migration of members from both production zones is well documented (Magnuson et al., 1994; Lutcavage et al., 1999; Block et al., 2001a, 2005; Rooker et al., 2006a), there is evidence for some degree of fidelity to natal areas, justifying the two-stock premise ("eastern" and "western" populations) and separate assessments used by the International Commission for the Conservation of Atlantic Tunas (ICCAT). Results of genetic and archival tagging studies support the two-stock hypothesis. Genetic differentiation and natal homing provide strong evidence for independence of *T. thynnus* stocks in the Gulf of Mexico and the Mediterranean Sea (Block et al., 2005; Boustany et al., 2006; Carlsson et al., 2007). Still, this assumption has been challenged by some because of the seasonal movement of *T. thynnus* across the 45°W meridian management boundary, as observed through catch data as well as electronic tagging. As a result, the supposition of only two spawning areas with a high degree of natal homing has been questioned (e.g. Lutcavage et al., 1999; Goldstein et al., 2007).

The controversy over the stock structure of *T. thynnus* is of particular concern because the spawning stock biomass of the smaller western stock (herein "western Atlantic" stock includes the Gulf of Mexico) has declined precipitously over the past few decades. Additionally, recent assessments indicate that spawning stock biomass is still in a state of greatly reduced abundance. Population estimates are far below reference levels despite over 20 years of strict regulations on fisheries in the western Atlantic (Standing Committee on Research and Statistics (SCRS), 2003, 2006). Even though the eastern stock (herein "eastern Atlantic" stock includes the Mediterranean Sea) is significantly larger and appears more stable, major uncertainties exist in Mediterranean landing statistics, CPUE indices, and spawning stock biomass, fueling debates regarding the condition of this stock (SCRS, 2003; Fromentin, 2003; Fromentin and Powers, 2005). Further, authors of the 2006 eastern *T. thynnus* stock assessment concluded that this stock was not being harvested at a sustainable level and was likely in a state of decline (SCRS, 2006).

Life history data for both eastern and western *T. thynnus* stocks have been supplied by scientists in both regions during the last decade, and an improved understanding of the basic biological parameters (e.g., age at maturity, fecundity, feeding, growth) is beginning to emerge. Considerable effort has been directed toward developing novel markers of natal origin and stock identity. Recent advances in molecular (hypervariable genetic markers or microsatellites) and biogeochemical methods (otolith chemistry) have afforded scientists new perspectives on the stock structure and movement of *T. thynnus*. Moreover, improved archival tags are allowing researchers to address key issues related to their life history and stock structure (e.g., site fidelity, spawning activity, trans-Atlantic movement). Combined with past information, new findings have significantly enhanced our understanding of

T. thynnus and reduced the degree of uncertainty in modeling efforts to manage this valuable species.

Several assessments or reviews of *T. thynnus* have been published over the last two decades. In the mid 1990s, extensive reviews were published (Magnuson et al., 1994; Mather et al., 1995). Both reviews contained useful information on general life history, historical evidence for stock structure, and the fishery history; however, a great deal of the life history information in these reviews is dated or treated superficially. Moreover, advances in genetics, otolith chemistry, and electronic tagging studies were not covered in earlier reviews. A recent review by Fromentin and Powers (2005) builds nicely on the previous publications and provides valuable information on the history of the fishery and the population status and management of *T. thynnus*. Still, a detailed synthesis of life history data pertinent to the management of this species is lacking. The purpose of this review is to comprehensively examine *T. thynnus* life history and stock structure by examining existing data bases as well as taking a meta-analysis approach with published data from various sources. In addition, the aim of this review is to emphasize recent studies that take advantage of novel approaches to address issues related to the biology of *T. thynnus*.

2. Life History

2.1. Geographic Location and Timing of Spawning

Inferences on the location and timing of spawning of *T. thynnus* are based primarily on patterns of larval distribution and histological examination of gonad condition. Two regional spawning areas or zones of production are widely recognized, one in the east and one in the west (Mediterranean Sea and Gulf of Mexico, respectively), and recent electronic tagging studies have confirmed the presence of these two principal spawning areas (Stokesbury et al., 2004; Block et al., 2005; Teo et al., 2007). Specific oceanographic conditions within each region appear important for spawning, and the actual location of spawning within each basin likely represents a balance between requirements of larvae and the physiological limitations of adults. The timing of spawning in both the east and west appears linked to temperature. Sea surface temperatures reported for *T. thynnus* on putative spawning grounds in the Gulf of Mexico and Mediterranean Sea range from approximately 22.6°C–27.5°C and 22.5°C–25.5°C, respectively (Karakulak et al., 2004a, 2004b; Garcia et al., 2005; Teo et al., 2007). Because the northern slope waters of the Gulf of Mexico are above the purported 24°C spawning threshold in early spring (Block et al., 2001a, 2001b, 2005; Teo et al., 2007), it is not surprising that *T. thynnus* begin spawning earlier in the Gulf of Mexico than in the Mediterranean Sea (April versus May) (Baglin, 1982; Clay, 1991; Nishida et al., 1998; Medina et al., 2002; Corriero et al., 2003; Karakulak et al., 2004a).

In the east, *T. thynnus* larvae have been collected throughout the Mediterranean Sea with the exception of the Ligurian Sea, northern Adriatic Sea, and Alboran Sea. The primary spawning areas in the Mediterranean Sea include the waters of southern Italy around Sicily (Sella, 1924, 1929a; Sanzo, 1932; Piccinetti and Manfrin, 1970; Tsuji et al., 1997; Nishida et al., 1998) and the Balearic Islands off the eastern coast of Spain (Duclerc et al., 1973; Dicenta, 1975; Rodriguez-Roda, 1975; Nishida et al., 1998; Garcia et al., 2003, 2005; Figure 1). In southern Italy, catch numbers of larvae are typically highest in the vicinity of the Sicilian Channel near Cape Passero and the Malta Channel. In the Balearic Archipelago, which represents a transitional zone (frontal boundary between Mediterranean and eastern Atlantic waters), peak densities have been reported from the Mallorca Channel (east of Ibiza) and south of Menorca (Garcia et al., 2003; 2005). Data from recent larval surveys in

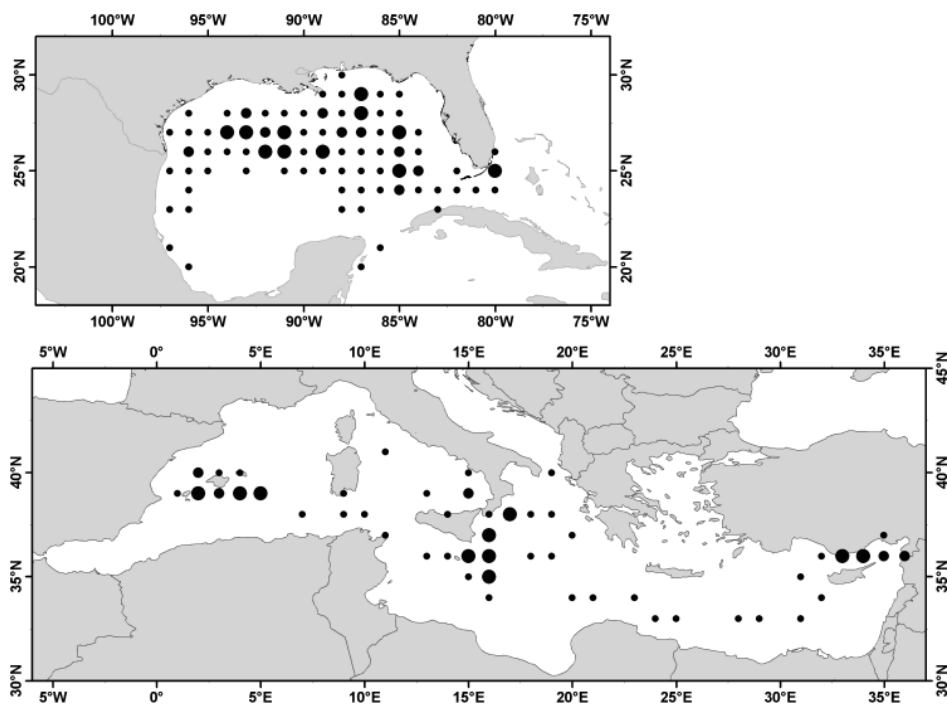


Figure 1. Distribution of Atlantic bluefin tuna (*Thunnus thynnus*) larvae in the Gulf of Mexico and Mediterranean Sea from the published literature (Garcia et al., 2003, 2005; McGowan and Richards, 1986; Nishida et al., 1998; Olvera-Limas et al., 1988; Oray and Karakulak, 2005; Richards, 1976, 1980, 1997; Richards and Potthoff, 1980; Tsuji et al., 1997) as well as unpublished SEAMAP data (1978, 1983, 1987, 1992, 2000) provided by S. Turner and W. Richards. The small circles denote catches of 1-4 larvae (per neuston or bongo net tow), the medium circles 5-10 larvae, and the largest circles 10 or more larvae. Coordinates rounded to whole degrees.

the eastern Mediterranean (Levantine Sea) indicate that *T. thynnus* also spawn in areas north of Cyprus along the coast of Turkey, with major catches near the Bay of Mersin (Karakulak et al., 2004a, 2004b; Oray and Karakulak, 2005).

Estimated spawning times in the Mediterranean Sea based on gonad condition indicate that intense spawning occurs during May–June in the eastern Mediterranean and during June–July in the central and western Mediterranean. Using the gonadal somatic index (GSI), Sarà (1964; 1973) reported peak spawning of *T. thynnus* from mid June and early July for specimens caught in traps from the central Mediterranean. Similarly, de la Serna and Alot (1992) reported increases in the GSI during July for *T. thynnus* caught in the western Mediterranean. By means of histological analysis, Sarasquete et al. (2002) observed post-ovulatory follicles in specimens caught in July in the western Mediterranean. The same type of analysis on females taken from around the Balearic Islands caught between June 26 and July 2 showed that all ovaries were in spawning stage (Medina et al., 2002). Recent histological and immunohistochemical investigations carried out by several investigators indicated that spawning occurs from mid June to early July in the central and western Mediterranean (Susca et al., 2001; Corriero et al., 2003). While predicted spawning times of *T. thynnus* from the central and western Mediterranean are similar, spawning appears to occur approximately one month earlier in the eastern Mediterranean. Based on histological analysis of ovaries and larval distribution data, *T. thynnus* spawn in the Levantine Sea as

early as May 20th (Karalulak et al., 2004a; Oray and Karakulak, 2005). Earlier spawning times in the eastern Mediterranean are likely linked to sea surface temperatures, which often approach the 24°C spawning threshold of tuna species (Block et al., 2001a; Teo et al., 2007) by mid to late May.

In the west, the highest concentrations of *T. thynnus* larvae have been collected in the northern Gulf of Mexico (Figure 1). Within this region, collection numbers peak in the general vicinity of the continental shelf break (26°–28°N latitude, 85°–94° W longitude) (Richards, 1976, 1997; Richards and Potthoff, 1980; Turner et al., 1996; Nishida et al., 1998). More specifically, larvae have been consistently collected in two regions: 26°–27° N, 91°–92° W and 27°–28° N, 85°–88° W. These areas of concentration are consistent with recent electronic tagging data, which indicate that spawning grounds of *T. thynnus* in the Gulf are located along the northern slope waters between the 200 m and 3000 m contours from 85°W and 95°W (Block et al., 2005; Teo et al., 2007). Catch and observer records from the NOAA Fisheries Service for commercial longline vessels are also highest in this region of the northern Gulf (Block et al., 2005). Apart from the northern Gulf, *T. thynnus* larvae have been reported from the southern Gulf to the Yucatan Channel (Richards and Potthoff, 1980; McGowan and Richards, 1986; Olvera Limas et al., 1988) and from the Straits of Florida to the Bahamas (Rivas, 1954; Richards, 1976; Richards and Potthoff, 1980; Brothers et al., 1983; McGowan and Richards, 1989). McGowan and Richards (1989) also collected *T. thynnus* larvae off the Carolina coast, but their presence was attributed to advection from spawning grounds in the Straits of Florida or Bahamas. In the northern Gulf, larvae are often concentrated in the intense frontal systems associated with the Loop Current (Figure 1), and areas of concentration often differ among surveys. Observed interannual variation in the catch is likely due to temporal variation in the spatial extent and shape of the Loop Current and associated features (eddies). As a result, a meta-analysis of larval collection data tends to show high concentrations in a broad region of the northern Gulf, even though areas of concentration during annual surveys are often restricted and patchy.

Assessment of reproductive condition of adult *T. thynnus* is limited in the western Atlantic; however, the GSI has been used to examine seasonal patterns of maturation and spawning within this region. Baglin (1982) determined GSI values for 403 female *T. thynnus* (194–290 cm CFL) and observed well-developed ovaries in April and May. GSI values were greater than 3.0% (>2% = mature) in both April and May, with GSI values for all other months less than 2.0%. Although not as comprehensive, other work by Baglin (1976) examined gonadal condition of females from the western Atlantic and reported peak GSI values in May. Brothers et al. (1983) back-calculated hatch dates of larvae aged using otoliths and indicated that spawning (~1 day prior to hatch) occurred from mid to late May; these dates are consistent with the GSI-based estimates.

Although the aforementioned data support the assertion that spawning areas are centered in the Gulf of Mexico and Mediterranean Sea, *T. thynnus* sometimes occur in areas outside these regions (e.g., Bahamas, central North Atlantic Ocean) during presumed spawning periods. Lutcavage et al. (1999) reported that 12 large *T. thynnus* (190- to 263-cm straight fork length (SFL)) tagged in New England in the fall relocated over a broad region of the central North Atlantic Ocean during the next May–July spawning period in the west, although there was some concern about premature release of some tags. Moreover, based upon continuous tracking of individuals, Block et al. (2005) observed that many adults (>200 cm curved fork length (CFL)) persisted in North American continental shelf and central Atlantic waters during spring and summer. The authors also noted that *T. thynnus* were present in the Bahamas during the spawning season, which is noteworthy since *T. thynnus* larvae have been collected in that region (Brothers et al., 1983; McGowan and

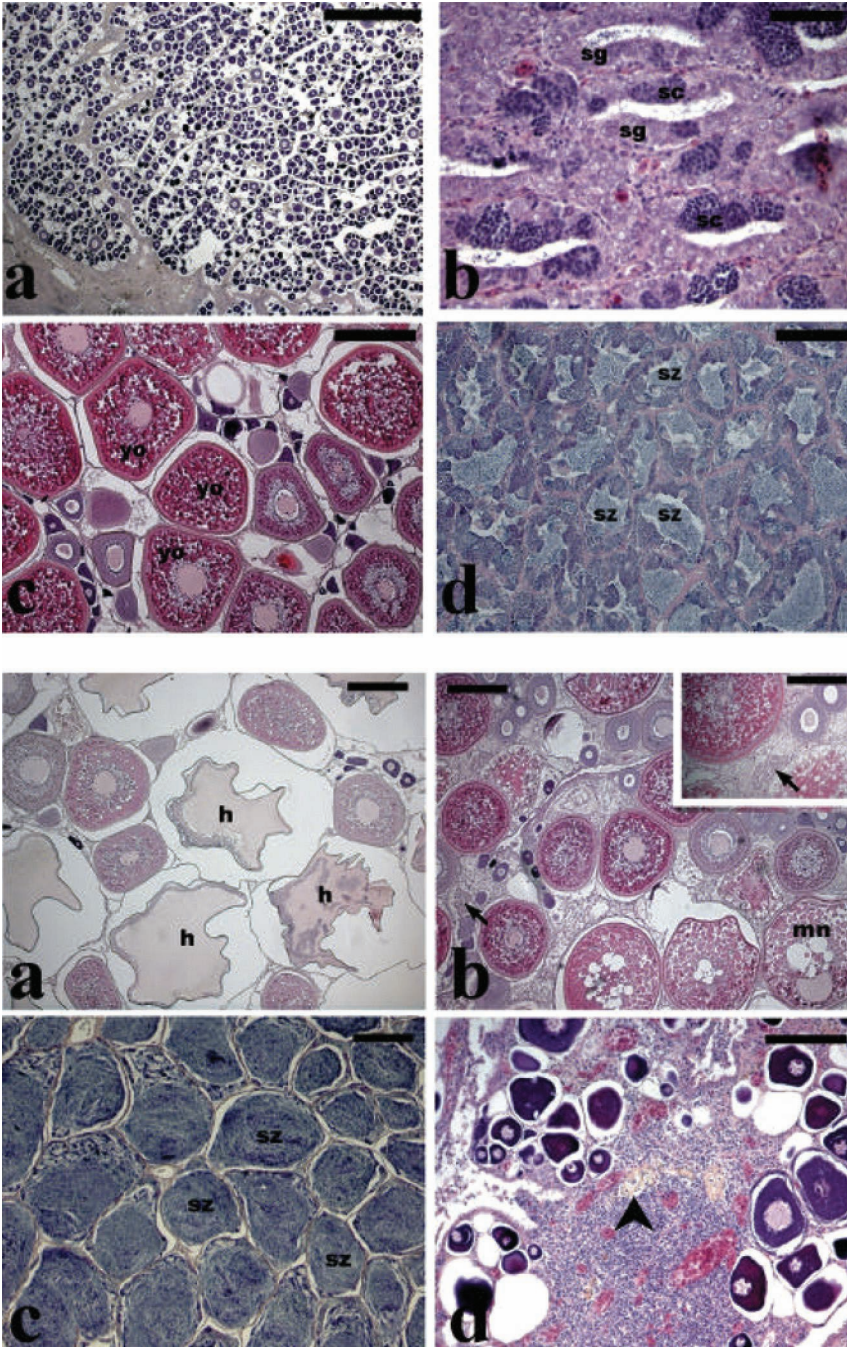


Figure 2. (A) Micrographs of the gonads from active non-spawning Atlantic bluefin tuna (*Thunnus thynnus*) captured in the Mediterranean Sea: (a) Ovary from an inactive fish showing only unyolked oocytes (bar = 1000 μm). (b) Seminiferous lobules from the testis of an inactive individual showing spermatogonia and spermatocytes (bar = 40 μm). (c) Ovary from an actively spawning specimen with advanced yolk oocytes (bar = 500 μm). (d) Seminiferous lobules from the testis of an active individual showing germ cells at all the spermatogenic stages. Luminal

Richards, 1989). The presence of *T. thynnus* outside of spawning areas during presumed spawning periods prompts three hypotheses: (1) spawning occurs in regions outside the Gulf of Mexico and Mediterranean Sea, (2) a fraction of the presumed adults are not reproductively mature, or (3) *T. thynnus* are not obligate annual spawners and sometimes “skip” spawning (Secor, 2006). Several years of directed sampling in the central Atlantic have failed to find spawning condition *T. thynnus*, and ichthyoplankton collections in the central North Atlantic have not produced any *T. thynnus* larvae (Fromentin and Powers, 2005). Still, scientific sampling of unknown spawning regions in the central North Atlantic and elsewhere is difficult, and therefore we cannot reject the first hypothesis of alternate spawning areas for *T. thynnus*. Consistent with the second hypothesis, Block et al. (2005) reported *T. thynnus* in the Gulf of Mexico larger in length than expected for individuals 8 years of age and speculated that many of the individuals observed outside the Gulf of the same age/size during the spawning season may not be reproductively mature. The last hypothesis regarding skipped spawning has not received intense scrutiny and may have some merit since reproductive schedules can exhibit large phenotypic plasticity in marine fishes (Rijnsdorp, 1989; Roff, 1991; Rideout et al., 2005). Nevertheless, Block et al. (2005) and Teo et al. (2007) observed that *T. thynnus* from both the Gulf of Mexico and Mediterranean Sea returned to the same spawning sites for up to three consecutive years.

2.2. Reproductive Biology

Ovaries of *T. thynnus* consist of ovigerous lamellae with follicles at different stages of development (Corriero et al., 2003). The simultaneous presence of all oocyte developmental stages during the spawning period (Medina et al., 2002; Corriero et al., 2003) indicates that *T. thynnus* has asynchronous oocyte development and, similar to other temperate and tropical tunas, is a multiple or batch spawner (Wallace and Selman, 1981; de Vlaming, 1983). Spawning frequency or interval for *T. thynnus* has been estimated at 1.2 days (Medina et al., 2002). This interval is similar to the observed frequencies of other members of the genus *Thunnus*: yellowfin tuna *T. albacares* (1.27 to 1.99; Itano, 2000; Schaefer, 1998), bigeye tuna *T. obesus* (1.05; Chu, 1999), and southern bluefin tuna *T. maccoyii* (1.62; Farley and Davis, 1998).

The testis of *T. thynnus* is comprised of lobules radiating from the longitudinal main sperm duct toward the periphery (Abascal et al., 2003). The testicular structure is cystic, each cyst being comprised of a clone of germ cells branched by the cytoplasm of Sertoli cells. Spermatogonia are distributed along the entire seminiferous lobules, thus indicating that the testis is of the unrestricted spermatogonial type in the classification described by Grier et al. (1980).

The reproductive cycle of *T. thynnus* can be reconstructed on the basis of the histological descriptions of the gonads of fish captured in different periods (Baglin, 1982; Medina et al., 2002; Santamaria et al., 2003; Corriero et al., 2003; Karakulak et al., 2004b) (Figure 2). In the

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spermatozoa are also visible (bar = 200 μm). sg, spermatogonia; sc, spermatocytes; yo, yolked oocytes; sz, spermatozoa. (B) Micrographs of the gonads from actively spawning *T. thynnus* (a) Ovary from an actively spawning fish with hydrated oocytes (bar = 500 μm). (b) Ovary from an actively spawning individual with both oocytes at migratory nucleus and post-ovulatory follicles (bar = 500 μm). (c) Testis from an actively spawning specimen showing the lumen of the seminiferous tubules filled with spermatozoa (bar = 300 μm). (d) Ovary from an inactive fish showing perinucleolar stage oocytes and δ atretic follicles (bar = 100 μm). All sections were stained with haematoxylin-eosin. Arrow, post-ovulatory follicle; arrowhead, late stage of atresia of yolked oocyte; h, hydrated oocyte; mn, migratory nucleus; sz, spermatozoa.

central and western Mediterranean, *T. thynnus* have been found to be reproductively inactive from August to April, when only unyolked oocytes are present in the ovaries, and mainly spermatogonia and meiotic cells have been found in the seminiferous epithelium. Active non-spawning individuals have been observed in May, with yolked oocytes in the ovaries and seminiferous lobules progressively filled with spermatozoa (Figure 2A). Hydrated oocytes and/or post-ovulatory follicles, signs of imminent and recent ovulation, respectively, have been found in actively spawning individuals captured in late June to early July (Figure 2B). From late July to September, *T. thynnus* are reproductively inactive, as ovaries show unyolked oocytes and late stages of atresia of yolked oocytes; only residual spermatozoa are present in the testes. The presence of actively spawning fish, with hydrated oocytes and/or post-ovulatory follicles, was reported in the eastern Mediterranean Sea from mid May to mid June, one month earlier than in the central and western Mediterranean (Karakulak et al., 2004b).

Fecundity. Estimated relative batch fecundity of *T. thynnus* is greater (>90 oocytes g^{-1} of body weight) than those estimated for other tunas in the genus *Thunnus*, which are typically less than 70 oocytes g^{-1} of body weight: *T. obesus* 31 oocytes g^{-1} (Nikaido et al., 1991), *T. maccoyii* 57 oocytes g^{-1} (Farley and Davis, 1998), and *T. albacares* 67 oocytes g^{-1} (Schaefer, 1998). Rodriguez-Roda (1967) reported a total fecundity of 97 to 137 oocytes g^{-1} body weight for 10 *T. thynnus* caught in eastern Atlantic along the coast of Spain. Moreover, a stereological study on 24 spawning *T. thynnus* from the Balearic Islands reported similar values, with an average batch fecundity of 93 oocytes g^{-1} body weight (Medina et al., 2002). They also noted that the spawning frequency of *T. thynnus* around the Balearic Islands was 1.2 days based on the postovulatory follicle method described by Hunter et al. (1985). Reported estimates of mean fecundity of large *T. thynnus* (>205 cm fork length (FL)) from the western Atlantic ranged from 30–60 million eggs (Baglin, 1982), which is considerably greater than estimated fecundity values of spawning *T. thynnus* from areas in the western Mediterranean and Strait of Gibraltar (ca. 13–15 million eggs, Medina et al., 2002). Maximum mean fecundity reported by Baglin and Rivas (1977) was approximately 45 million eggs, albeit that study predicted fecundity could reach 75 million eggs for a 25-year-old female.

Size and age at maturity. Data on size and age at maturity for *T. thynnus* are limited and the large disparity between maturity schedules for eastern and western Atlantic stocks has been debated in the literature. In the eastern Atlantic, Rodriguez-Roda (1967) estimated that 50% of female *T. thynnus* in the Mediterranean Sea were reproductively active at approximately 103 cm CFL¹ (age 3), and 100% maturity was reached between 115 and 121 cm CFL (age 4 or age 5). Findings from this study were corroborated recently by Corriero et al. (2005). These authors reported that 50% of *T. thynnus* in the Mediterranean Sea reached sexual maturity at 104 cm SFL¹ (age 3 or age 4) and 100% at 130 cm SFL (age 5; Figure 3). Reported values differ from inferences drawn from electronic tagging data, which suggests some eastern *T. thynnus* may not initially spawn until they are considerably older. Block et al. (2005) reported that adolescent *T. thynnus* tagged off North Carolina and destined to return to the Mediterranean Sea during the spawning season did not reenter the Mediterranean until they were larger than 205 cm CFL (ages 9 to 10) (see Section 3.2).

In the western Atlantic, histological examination of ovaries from females showed delayed maturation schedules, and individuals were unlikely to reach sexual maturity before age 8 (Baglin, 1982). Although scrutinized by Clay (1991), the longstanding values used

¹Conversion of curved fork length (CFL) to straight fork length (SFL); $SFL = 0.973 * \text{curved fork length CFL}$ (Van Voorhees et al., 2006, SCRS 081).

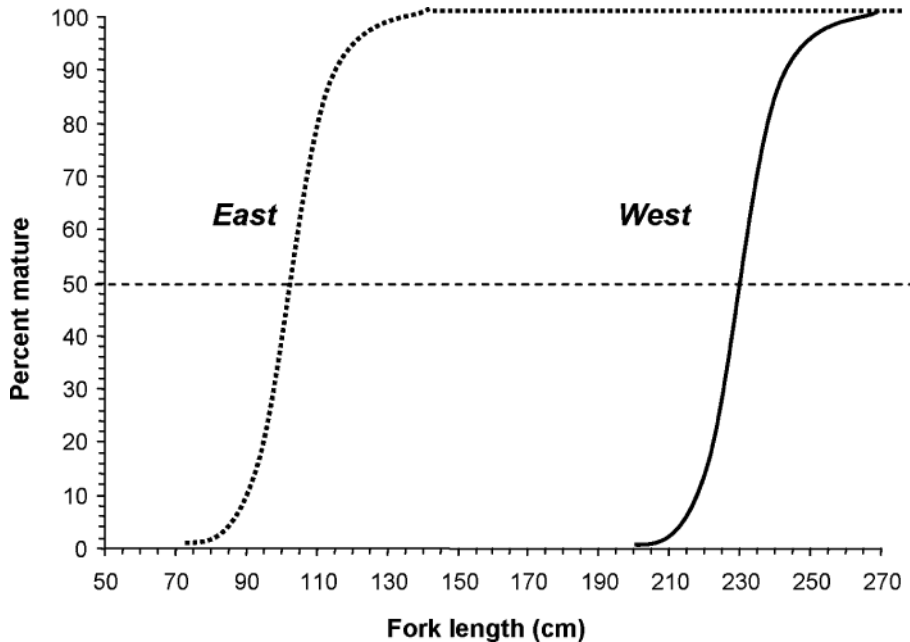


Figure 3. Percentages of mature eastern and western Atlantic bluefin tuna (*Thunnus thynnus*) plotted as functions of length. Estimates for the eastern Atlantic are based on histological analysis (Corriero et al., 2005), and those for the western Atlantic are based on size-frequency data from U.S. and Japanese pelagic longline vessels (Diaz and Turner, 2006), respectively.

for age of and size at sexual maturity of *T. thynnus* in the west are approximately age 10 and 200 cm CFL (Magnuson et al., 1994). Nemerson et al. (2000) used size-frequency analysis to characterize *T. thynnus* caught in the Gulf of Mexico from 1980–1982 and reported that more than 99% of the fish caught on the spawning grounds were age 8 or older (> 135 kg). Similarly, Diaz and Turner (2006) examined size-frequency data from U.S. and Japanese longline fleets in the Gulf of Mexico from January to June and reported that approximately 98% of all *T. thynnus* in the Gulf of Mexico were age 9 or older. They also noted that the age at 50% maturity was approximately age 11 or 12. Based upon the model and size-frequency evidence, it appears that the western spawning stock is comprised of larger, late-maturing individuals. Based on the length distribution of spawning adults in the Gulf of Mexico, Block et al. (2005) noted that a significant fraction of *T. thynnus* from the western Atlantic may initially spawn at even larger sizes and older ages than those estimated by Baglin (1982) and Nemerson et al. (2000), reporting a mean size of fish entering the Gulf of Mexico of 241 ± 28 cm CFL (corresponding to age 11), which is consistent with the results of Diaz and Turner (2006). Recently, Goldstein et al. (2007) observed that age 7–8 *T. thynnus* collected from the Gulf of Maine were reproductively mature, which is markedly different than length-based assessment of maturity for *T. thynnus* collected in the Gulf of Mexico. The presence of mature females at age 7–8 in the western Atlantic is interesting and unexpected, and the authors noted that earlier maturing individuals of Mediterranean origin may have been part of the Gulf of Maine sample.

Reproductive behavior. *Thunnus thynnus* display distinct behaviors during the spawning phase, most noticeably with changes in diving times and depths (Block et al., 2001a;

Teo et al., 2007). Upon entry into the Gulf of Mexico during spawning runs, *T. thynnus* show deep-diving behaviors, which likely provide access to cool, oxygen-rich waters as the fish travel to breeding grounds (Stokesbury et al., 2004; Teo et al., 2007). Once on the spawning area, *T. thynnus* make shallow oscillatory dives at night with frequent visits to the surface. Similar behaviors have been observed for *T. orientalis* (Kitagawa et al., 2006) and *T. albacares* (Schaefer, 1998, 2001) during the breeding phase. *Thunnus thynnus* maintain this behavior for approximately 20 days, and mature individuals tagged in the western Atlantic were observed on spawning grounds in the Gulf of Mexico for an average of 39 ± 11 days (Block et al., 2001a; Teo et al., 2007). Maximum diving depths of *T. thynnus* are significantly less (<200 m versus >500 m) during the spawning phase than observed during entry to and exit from spawning grounds in the west. Moreover, movement paths of spawning adults are often limited in scope relative to typical dispersion patterns during the non-spawning phase (Teo et al., 2007), suggesting directed movements into and away from spawning grounds. Once on the spawning ground, aggregations of *T. thynnus* individuals of different sizes and/or ages have been observed during actual spawning events, with schools becoming more size specific after the spawning phase in the Mediterranean Sea (Sarà, 1983).

2.3. Feeding

Thunnus thynnus consume a wide variety of prey and have been described as opportunistic feeders. As larvae and small juveniles, their diet is probably similar to that of *T. orientalis* in the Pacific Ocean, which is comprised primarily of zooplankton with copepods as the main stomach item (Uotani et al., 1981, 1990). Moreover, larvae are capable of feeding on other fish larvae by the flexion stage (~7 mm SL; Miyashita et al., 2001). The diet of older juveniles and adults is comprised mainly of fishes, cephalopods (mostly squid), and crustaceans (Sarà and Sarà, 2007). These categories may include numerous species, and the particular composition is determined principally by location. They may pursue and consume individual prey items, but with respect to the most common prey items they use ram feeding (swimming through a school of fish with their mouths open). In the western Atlantic, the most important items by frequency and weight are small schooling fishes: Atlantic herring *Clupea harengus*, Atlantic mackerel *Scomber scombrus*, sand lances *Ammodytes* spp., and silver hake *Merluccius bilinearis* (Nichols, 1922; Crane, 1936; Bigelow and Schroeder, 1953; Dragovich, 1970; Mason, 1976; Holliday, 1978; Eggleston and Bochenek, 1990; Chase, 2002). In the eastern Atlantic and Mediterranean Sea, European sprat *Clupea sprattus*, European anchovy *Engraulis encrasicolus*, and European pilchard *Sardina pilchardus* are particularly important (Priol, 1944; Oren et al., 1959; Morovic, 1961; De Jager et al., 1963). At tropical latitudes, porcupinefish *Diodon* sp. and flying gurnard *Dactylopterus* sp. were the dominate items observed in the stomachs of *T. thynnus* (Krumholz, 1959; Dragovich, 1970). Demersal fishes and invertebrates are often found in the stomachs of *T. thynnus*, especially in nearshore environments. While no single taxon dominates, as a group, demersal organisms may comprise as much as 20% of the stomach contents by number (Chase, 2002). Finally, *T. thynnus* >230 cm CFL may eat large individual prey items (e.g., bluefish *Pomatomus saltatrix* or spiny dogfish *Squalus acanthias*) (Mathews et al., 1977; Chase, 2002).

Published studies of *T. thynnus* diets have been primarily descriptive and cross-sectional in scope, and the tendency for these fish to regurgitate during capture complicates dietary assessments and associated bioenergetic and ecosystem modeling efforts. Overholtz (2006) used meta-analysis to estimate the daily ration of *T. thynnus* and reported a mean of 3.2%

of body weight (range: 1.0 to 4.7%). This value is comparable to daily ratio levels reported for *T. albacares* in the Pacific Ocean (Olson and Boggs, 1986). Due to regurgitation effects, mean daily ration for *T. thynnus* may be underestimated, while the relative importance of certain prey that are difficult to expel (e.g., *Diodon* spp., or larger prey items) may be overrepresented. Therefore, diets of *T. thynnus* reported in the literature may inaccurately portray trophic linkages of that taxon in large marine ecosystems. Studies using dietary markers such as stable carbon and nitrogen isotopes, which provide a longer-term integrated measure of diet, indicated that trophic position of *T. thynnus* is size dependent and ranges from 3.0 to 4.8 (Estrada et al., 2005, Sarà and Sarà (2007). Also, Estrada et al. (2005) reported that certain prey items (e.g., nektonic crustaceans) are underrepresented in larger *T. thynnus*, which feed at a trophic position of 4.0 or greater. This value is nearly a full trophic step higher than those of congeners such as *T. albacares*, but similar to those of sympatric elasmobranchs (Estrada et al., 2003; Rooker et al., 2006b).

The depth distributions of *T. thynnus* and other tunas are inherently linked to foraging activity, and vertical position within the water column is often regarded as an indicator of where the fish are feeding. Archival tagging results indicate that *T. thynnus* spend a considerable amount of time in the upper mixed layer, particularly on the inner continental shelf where diving depths are limited by the bathymetry (Block et al., 2001a). Feeding in the mixed layer above the thermocline is common for both tropical and temperate tunas, and vertical use patterns may vary temporally as a function of shifts in prey distribution (Musyl et al., 2003; Kitagawa et al., 2006). While *T. thynnus* spend the majority of their time in waters less than 200 m and often frequent water depths less than 50 m, they are capable of making deeper dives to 1000 m when in offshore waters of the North Atlantic (Block et al., 2001a; Stokesbury et al., 2004; De Metrio et al., 2005). The frequency of deep dives appears greatest for *T. thynnus* when they occupy the warmest waters of the Gulf of Mexico (Block et al., 2001a; Teo et al., 2007). Since *T. thynnus* are endothermic, the frequency of deep dives in the Gulf may be related to thermal physiology rather than simply feeding. Block et al. (2005) hypothesized that *T. thynnus* are thermally stressed while in the warm waters of the Gulf, and thus individuals potentially dive beneath the thermocline to avoid overheating.

2.4. Age, Growth, and Mortality

Current assessments for *T. thynnus* are based on age-structured models, with catch-at-age inputs derived from age slicing applied to independent growth curves for each stock. Methods used to estimate age and growth of *T. thynnus* have been based on the examination of calcified structures, modal analysis of length frequencies, and tagging studies (Table 1). The first two methods have been applied successfully to age both juveniles and adults; however, slower growth rates later in life present difficulties in age interpretation from calcified structures, and length analysis is suitable only when modes (age groups) are identifiable. Mark-recapture methods are often useful, but due to uncertainties in the initial age of a fish at release and logistical constraints, age and growth data derived from this method are limited. Because of biases associated with any single approach, studies based on several methods, or at least on several calcified structures, are common for this species (Westman and Neville, 1942; Mather and Schuck, 1960; Farrugio, 1980; Farber and Lee, 1981; Lee et al., 1983; Hattour, 1984; Cort, 1991).

Several different calcified structures have been used to estimate the age of *T. thynnus*, and the most common structures include otoliths (e.g., Brothers et al., 1983; Foreman,

Table 1

Overview of age and growth studies conducted on Atlantic bluefin tuna (*Thunnus thynnus*) from the eastern and western regions. Estimated growth parameters and age-length keys shown. Age-length relationships were based on von Bertalanffy (VB) growth model or mean length-at-age (MLA) (Continued)

	Westman and Neville (1942)	Mather and Schuck (1960)	Caddy et al. (1976) and Butler et al. (1977)	Farber and Lee (1981)	Hurley and Iles (1983)	Parrack and Phares (1979)	Turner and Restrepo (1994)
Area	W. ATL (NE US) MLA	W. ATL (NE US) MLA	W. ATL (Canada) VB	W. ATL (Mid Atlantic) VB	W. ATL (Canada, US) VB	W. ATL W. ATL VB	W. ATL W. ATL VB
Age material	Length str. & scales	Scales & caudal vert.	Otolith sect. males	mark-recapture	Otolith sect. males	mark-recapture	mark-recapture
L_{∞}	371.0	371.0	286.6	313.0	277.8	313.0	382.0
K	0.069	0.134	0.134	0.120	0.169	0.090	0.079
T_0	-1.373	-0.328	-0.800	-0.140	0.254	-0.960	-0.707
Ages with >3 indiv. sampled	1 to 4	1 to 10, 12, 13	all	all	2, 4-6, 11, 13-28	2, 4-6, 15-30	
Mean fork length (cm)	Curved	Straight	Straight	Straight	Straight	Straight	Straight
Data	Observed	Observed	Estimated (4)	Estimated (4)	Observed	Estimated	Estimated
Age	1	55.9	57.0	40.0	64.0	50.6	48.2
	2	85.0	77.0	70.9	75.5	73.2	73.5
	3	105.2	95.0	98.3	77.3	93.8	97.0
	4	117.6	114.0	122.5	113.3	112.7	118.6
	5	147.8	135.0	144.1	147.1	129.9	138.6
	6	148.3	155.4	163.2	157.9	145.7	157.1
	7	157.5	161.6	180.1	173.3	160.1	174.2
	8	174.4	177.0	195.2	253.0	173.3	190.0
	9	186.1	190.0	208.5	223.7	185.3	204.6
	10	203.4	201.0	220.3	234.0	196.3	218.0
	11	224.5	223.8	230.8	234.5	206.3	230.5
	12	233.7	231.7		234.5	215.5	242.0
	13	243.3	238.6		256.3	223.9	252.6
	14	248.0	244.6		253.5	231.6	262.5
	15		249.9		262.9	238.6	271.5
	16		254.5		262.5	245.0	279.9
	17		258.5		262.5	250.8	287.7
	18		262.1		264.0	256.2	294.9

(Continued on next page)

Table 1
 Overview of age and growth studies conducted on Atlantic bluefin tuna (*Thunnus thynnus*) from the eastern and western regions. Estimated growth parameters and age-length keys shown. Age-length relationships were based on von Bertalanffy (VB) growth model or mean length-at-age (MLA) (Continued)

Western Atlantic	Westman and Neville (1942)	Mather and Schuck (1960)	Caddy et al. (1976) and Butler et al. (1977)	Farber and Lee (1981)	Hurley and Iles (1983)	Parrack and Phares (1979)	Turner and Restrepo (1994)
19			249.4		267.5	261.1	301.5
20			265.1		268.7	265.5	307.6
21			267.8		268.3		
22			270.2		270.4		
23			272.3		270.1		
24			274.1		271.5		
25			275.6		272.2		
26			277.0		274.4		
27					274.4		
28					272.5		
29					272.7		
30					273.7		

(1) Probably calculated at the beginning of the year or during slow growth/translucent band formation.

(2) Estimated from length structure for ages 1 to 8 and observed from spines from 9 to 15 years old.

(3) Mean fork length at age was obtained by applying length distributions of catches to the age length.

(4) Growth parameters estimated using ages 1–4 from Mather and Schuck (1960); * based on straight fork length.



Figure 4. Calcified structures of Atlantic bluefin tuna (*Thunnus thynnus*) used for age estimation: (a) vertebrae (estimated age = 9), (b) dorsal spine (estimated age = 8), (c) sectioned sagittal otolith (estimated age = 9).

1986; Itoh et al., 2000; Megalofonou, 2006; Megalofonou et al., 2003) and spines (e.g., Compeán-Jimenez and Bard, 1983; Cort, 1991; Mather et al., 1995; Figure 4). Otoliths have been used to estimate growth during larval, juvenile, and adult phases, and these aragonitic structures have the advantage that the central nucleus is not resorbed or obscured with age (Hurley and Iles, 1983). Spines are commonly used to age *T. thynnus* even though age estimates from spines are complicated by the resorption of the medullar cavity from age 3. Still, the approach has proven useful in the direct age determination of *T. thynnus*, particularly by researchers working on the eastern Atlantic stock (Compeán-Jimenez and Bard, 1983; Cort, 1991; Mather et al., 1995; Rodríguez-Marín et al., 2004). Growth increments are also readily apparent on vertebrae (Figure 4), but as is the case for otoliths, growth increments on vertebrae become tightly aligned at the margin (edge of the centrum)

at about age 9 or 10, reducing the reliability of age determination from that structure (Lee et al., 1983). Prince et al. (1985) presented a modified method using vertebra sections, and the alternative was applied for age determination of larger (older) *T. thynnus*. Scales have also been used for age determination of *T. thynnus*, but their efficacy was limited to the youngest fish, up to 4 or 5 years (Mather and Schuck, 1960).

Growth and mortality of *T. thynnus* during the larval phase has been determined from age data from otolith microstructure analysis. Scott et al. (1993) reported that growth was linear during the larval phase (~ 2 –10 days) at a rate of 0.3–0.4 mm d⁻¹. Similar rates have been reported for congeners from temperate and tropical regions: *T. orientalis* (0.33 mm d⁻¹; Miyashita et al., 2001), *T. albacares* (0.47 mm d⁻¹; Lang et al., 1994), and *T. maccoyii* (0.28–0.36 mm d⁻¹; Jenkins and Davis, 1990; Jenkins et al., 1991). Otolith-derived ages have been used in conjunction with abundance data (i.e., catch curves) to estimate natural mortality rates of *T. thynnus*. Natural mortality (M) or total mortality (Z) of *T. thynnus* during early life is due primarily to starvation and predation, and Z d⁻¹ during the larval stage has been estimated from declines in abundance over time. Scott et al. (1993) estimated a Z of 0.20 d⁻¹ for larvae from the western stock, and rates are lower than values reported for more tropical tunas during comparable periods: *T. albacares* ($Z = 0.33$ d⁻¹; Lang et al., 1994) and *T. maccoyii* ($Z = 0.66$ d⁻¹; Davis et al., 1991).

There have been several studies of growth and mortality of *T. thynnus* during the early juvenile period (age 0). Based on otolith microstructure analysis, Brothers et al. (1983) reported a growth rate of 1.4 mm d⁻¹ for juveniles in the western Atlantic (267–413 mm FL; ca. 70–200 d). This rate is comparable to earlier work based on progressions of modes in length-frequencies which ranged from 1.0 to 1.6 mm d⁻¹ (Rivas, 1954; Mather and Schuck, 1960; Furnestin and Dardingac, 1962). Recent estimates of growth for juvenile *T. thynnus* (85–555 mm FL) from the Mediterranean Sea are markedly higher, with a mean growth rate of 4.7 mm d⁻¹ (Megalofonou, 2006). Similarly, Itoh et al. (2000) reported greater rates of growth for juvenile *T. orientalis* (<240 mm FL, <72 d) in the Pacific Ocean, with a mean growth rate of 3.4 mm d⁻¹. Rapid growth of this magnitude has been reported for other tunas as well, with rates of 3 to 4 mm d⁻¹ reported for several taxa (Tanabe et al., 2003). Estimates of total mortality have been reported for juvenile *T. thynnus* (\sim age 0 to age 2) from waters around the Iberian Peninsula, with Z ranging from 0.51–0.70 (Rodríguez-Marín et al., 2005). Also, estimates of M have been reported for other juvenile tunas and, as expected, M values are relatively high during the early juvenile stage. Natural mortality rates of small *T. albacares* (<300 mm) and skipjack tuna *Katsuwonus pelamis* range from 5–7 yr⁻¹ and 6–13 yr⁻¹, respectively (Hampton, 2000; Fonteneau and Pallares, 2005). Reported M values for juvenile (<400 mm) *T. obesus* range from <1 yr⁻¹ (Fonteneau and Pallares, 2005) up to 4 yr⁻¹ (Hampton, 2000). Work to date indicates that mortality of tunas during the juvenile phase is largely a function of size or age rather than species or habitat (Hampton 2000). Therefore, natural mortality of *T. thynnus* during the first year of life is likely within the range reported for other tunas.

Age structure of adult *T. thynnus* has been studied in both the eastern and western Atlantic, and estimated growth rates are relatively similar between and within regions during the first five years of life (Table 1). Mean observed length at age (based on averaging estimates from studies shown in Table 1) of *T. thynnus* at age 1, age 2, and age 3 in the eastern Atlantic and Mediterranean were 54, 77, and 103 cm straight FL. Similarly, mean estimates of length at age 1 and age 2 in the western Atlantic were 53 and 75 cm FL, respectively. At age 3, a modest decline in length at age (ca. 12 cm) occurs in the western Atlantic. Estimated length at age of *T. thynnus* at ages 4 and 5 were again similar in both the eastern and western Atlantic: age 4 (118 and 118 cm FL, respectively), age 5 (135 and

139 cm FL, respectively). After age 5, growth trajectories of *T. thynnus* show marked differences between the eastern and western Atlantic, with the length at age being greater in the western Atlantic than the eastern Atlantic. At age 10, mean size in the western Atlantic was 212 cm FL compared to 200 cm FL for the eastern Atlantic. The general trend of greater length at age in the western Atlantic is exhibited in the growth models used for ICCAT assessments in the east (Cort, 1991) and west (Turner and Restrepo, 1994). Nevertheless, it should be noted that accepted growth curves for the eastern and western Atlantic are based on different age determination approaches (west: tagging data; east: length-based cohort analysis and spines, Figure 5). Although reported L_{∞} and K parameters differ within each region, in general the L_{∞} estimates are higher and the K estimates lower in the west (Table 1). Analyses that integrate more than one hard part or approach (direct age determination, length-based modeling, and mark-recapture methods) into a unified growth model (see Eveson et al., 2004, for *T. maccoyii*) are critically needed for both regions to clarify the relative magnitude of differences in growth between and within eastern and western Atlantic stocks.

Seasonal and sex-specific differences in growth also occur for *T. thynnus*. The existence of a slowdown in growth during the winter has been confirmed for both juveniles (Mather and Schuck, 1960; Furnestin and Dardignac, 1962; Farrugio, 1980; Cort, 1991) and adults (Tiews, 1963; Rodriguez-Roda, 1964a; Butler et al., 1977), and also for *T. orientalis* in the Pacific Ocean (Bayliff, 1993). Seasonal variations in length and growth rates of older *T. thynnus* are less apparent, probably due to the weak relationship between age and length for individuals more than 15 years of age (Hurlbut and Clay, 1988). Sex-specific differences

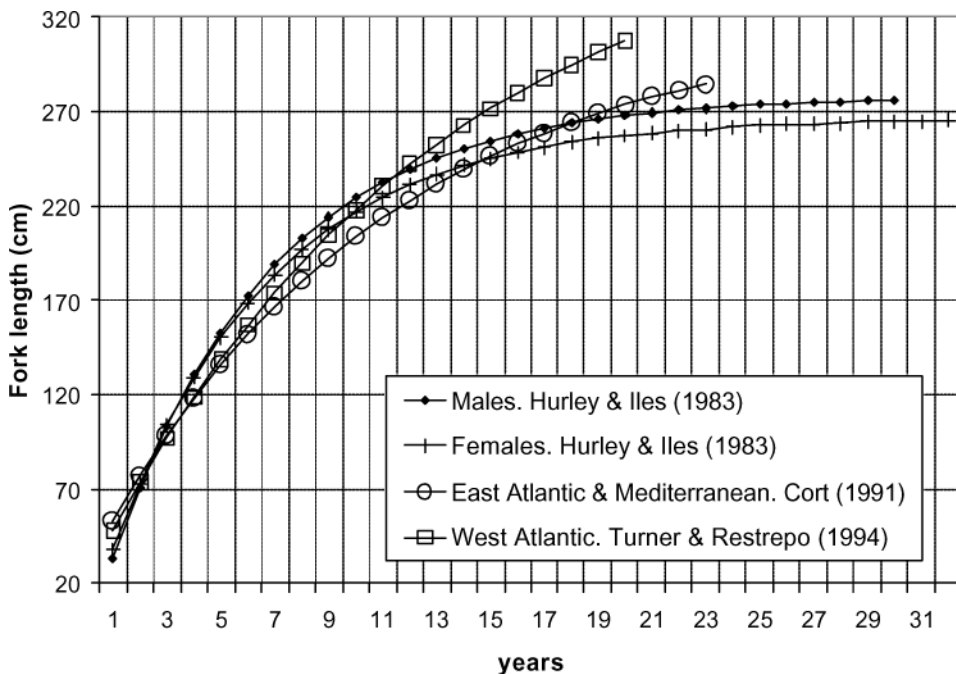


Figure 5. von Bertalanffy growth curves of Atlantic bluefin tuna (*Thunnus thynnus*) by sex and region. Also, growth curves (sexes combined) used for eastern and western Atlantic stock assessment by ICCAT (Cort, 1991, and Turner and Restrepo, 1994, respectively).

both in length at age and weight at age have been reported, with differential growth in weight being more pronounced between males and females. Males grow more rapidly than females and reach a slightly greater size at a given age, with these differences becoming apparent by approximately age 10 (Rivas, 1976; Caddy et al., 1976; Table 1, Figure 5).

To date, no robust age validation study has been published for *T. thynnus*. Bomb radiocarbon dating of archived otoliths has recently been used to validate the age of long-lived fishes (Campana, 2001). This approach, which can be used to confirm age interpretations at varying levels of resolution, is particularly useful in establishing longevity. It was successfully used by Kalish et al. (1996) to validate otolith-based estimates of longevity in *T. maccoyii* (~30 years). A similar but preliminary study of *T. thynnus* otoliths sampled from the North Atlantic (Neilson and Campana, 2006) confirmed previous otolith-based age interpretations, but also indicated moderately greater longevity and smaller sizes at ages (lower *K*, greater age at maturity) than previously recognized. Sample size was small, but should the result be upheld by future work, otolith-based age determination could lead to valid interpretations and provide much improved inputs for biological reference points in fishery assessment models.

3. Movement and Stock Structure

In addition to conventional tagging, recent advances in electronic tagging, otolith chemistry, and genetics have significantly enhanced our current understanding of *T. thynnus* movement and stock structure. Although researchers have known about trans-Atlantic movement for many decades (e.g., Sella, 1927, 1929b), current work indicates that mixing of the eastern and western Atlantic stocks is substantially greater than previously assumed. Moreover, these novel approaches are providing valuable insight on home range dynamics, seasonal movement, and the stock structure of *T. thynnus* both within and between management units.

3.1. Conventional Tagging

Mark-recapture studies with identification tags (“conventional tagging”) have historically provided valuable information on key aspects of the biology of *T. thynnus*. In the western North Atlantic where most of the effort has been concentrated (40,743 releases between 1954 and 2005), tagging by U.S. researchers can be classified into two historical periods. Prior to the early 1980s, most of the fish were obtained from commercial purse seine vessels and the tagging was conducted primarily by scientists in New England waters. During that period, most of the *T. thynnus* tagged were “school size,” typically <61 kg or <120 cm CFL. Since the early 1980s, tagging has been a cooperative effort involving non-scientific anglers, which has resulted in a greater proportion of medium (61–140 kg, 120–205 cm CFL) and giant (>140 kg, >205 cm CFL) category *T. thynnus* being tagged. In addition, effort has shifted to more southern areas off North Carolina and South Carolina. The program was initiated at the Woods Hole Oceanographic Institute in 1953 and later combined efforts with NOAA Fisheries in 1973. In 1980, NOAA’s Southeast Fisheries Science Center took control of the program, which is now called the Cooperative Tagging Center (CTC). A more detailed description of the history of the CTC can be found in Scott et al. (1990). Canadian researchers have also tagged *T. thynnus* in the western Atlantic, this effort being concentrated in the 1990s with over 1,700 medium- and giant-category individuals tagged at latitudes north of 40°N. By comparison, eastern Atlantic tagging efforts have been sporadic with shorter and more directed tagging episodes carried out independently by organizations of

several countries (Spain, Italy, Greece, and to a lesser extent, Japan and Ireland). Smaller *T. thynnus* were typically targeted (school and medium size categories) in the eastern Atlantic, and total number of tags deployed is about one-third of that in the western Atlantic (14,951 through the end of 2005). Overall recapture rate, pooled across programs and years, has been approximately 9%.

Of all the uses of tagging data, inferences about trans-Atlantic movements have been the most controversial because of the implications to the two-stock premise (Magnuson et al., 1994). Definitive statements about trans-Atlantic movements have been hampered by problems that are typical of tagging studies, which have received disproportionately low attention given the overall effort devoted to tagging fish. Because recaptures are fishery-dependent, spatial and temporal variations in effort and gear deployments influence recaptures, and thus it is difficult to compare recapture rates by time and/or location. This problem has typically been handled by making comparisons with relative (rather than absolute) recapture rates. Using this approach, tagging data indicate that the majority of recaptures (between 70% and 99%) were within tagging areas in both the eastern and western Atlantic regardless of time at liberty (Table 2). The concentration of recapture sites in the same management district where individuals were tagged is central evidence underlying the two-stock premise (Magnuson et al., 1994).

To further explore movement patterns of *T. thynnus*, the complete tagging database was obtained from the CTC, and patterns of movement were further investigated here by quantifying movement among the ICCAT sampling areas. Because past assessments have failed to fully explore time at liberty and size/age effects on movement among sampling areas, the following assessment partitions recaptures into two at-large categories (times at liberty less than and greater than one year) and three age categories (<4, 4–8, >8 years; Fromentin, 2001).

For tags deployed in the western Atlantic, proportions of recaptures within the west were relatively high for *T. thynnus* at large less than one year (Table 2). Over 99% of the recaptured *T. thynnus* juveniles (<4 years) tagged in the western Atlantic were recaptured in the western Atlantic. Although numbers were limited for the older age categories, a small fraction of the recaptured individuals ages 4 to 8 were recaptured in the eastern Atlantic, all in the Bay of Biscay (3.0%). For adult *T. thynnus* (>8 years) tagged in the western Atlantic and at liberty for less than one year, 92.4% were recaptured in the Gulf of Mexico or the western Atlantic (U.S. to Canada); small numbers of recaptures occurred in the Mediterranean Sea (4.2%) and the central North Atlantic (3.4%). This clearly shows that long-distance movements to either spawning or feeding grounds may occur over short periods (<1 year), but these individuals may represent only a small part of the overall population. In addition, non-reporting of western tags from fisheries in the eastern Atlantic and Mediterranean Sea may be an issue. The low level of trans-Atlantic movement reported here for *T. thynnus* at large <1 year is consistent with rates reported by Fromentin (2001), which indicated that west to east trans-Atlantic migration rates were 2.3%. Inferences based upon tagged *T. thynnus* at large >1 year showed more widespread distributions, with trans-Atlantic mixing rates considerably greater than reported previously. A substantial fraction (22.8%) of 4- to 8-year-old *T. thynnus* tagged in the western Atlantic crossed the 45°W meridian and were present in the Mediterranean Sea, Bay of Biscay, or the region west of Gibraltar (Table 2, Figure 6). Similarly, 12.6% of adults (> age 8) tagged in the western Atlantic were recaptured in the Mediterranean Sea (8.2%) or west of the Strait of Gibraltar (4.2%).

Evidence of movement in the eastern Atlantic is more limited due to the lack of tagging and recaptures of older *T. thynnus*. Data for juvenile (<4 years) *T. thynnus* at large

Table 2

Conventional tagging data comparison of relative recapture rates of Atlantic bluefin tuna (*Thunnus thynnus*) between different age groups within different recapture areas (years 1954 to 2005 pooled). Shaded blocks identify recaptures within the release area. Age groups are according to Fromentin (2001) based on size: <4 (juvenile in the east or west), 4 to 8 (juvenile in the west or adult in the east), >8 (adult in west or east), ? = no size data were available

	Western Atlantic				Eastern Atlantic				
	Age-Class = Total Releases	<4 26536	4 to 8 5859	>8 5706	? 4384	<4 14668	4 to 8 13	>8 24	? 251
<365 Days-at-large									
Gulf of Mexico		99.1%	96.2%	8.5%	0.3%				
U.S. & Can.		0.1%	0.8%	83.9%	98.4%	0.3%			
Cen. N. Atl. & Car.		0.7%	3.0%	3.4%	0.7%				
Bay of Biscay		0.04%		4.2%		35.8%			
W. of Gibraltar		0.04%				3.6%			
Med. Sea		2461	133	118	304	51.2%	100%		
Other areas						9.2%			
Subtotal						338	4	0	0
>365 Days-at-large									
Gulf of Mexico		0.2%	1.5%	6.3%	2.0%				
U.S. & Can.		91.8%	67.4%	76.0%	84.2%	9.5%			
Cen. N. Atl. & Car.		1.3%	5.3%	1.9%	1.9%				
Bay of Biscay		5.3%	3.0%		5.9%	66.4%			
W. of Gibraltar		0.2%	9.9%	4.4%	1.0%	4.3%			
Med. Sea		0.8%	9.9%	8.2%	3.0%	13.8%	100%	100%	100%
Other areas		0.4%	3.0%	3.2%	2.0%	6.0%			
Subtotal		1274	132	158	101	116	1	1	1
Total		3735	265	276	405	454	5	1	1

Definition of recapture areas: Gulf of Mexico = bounded by 20°N in the Caribbean Sea and 81°W in the Straits of Florida; U.S. and Canada = bounded by 20°N and 60°W; central North Atlantic and Caribbean = between 40°W and 60°W and north of 30°N, and areas south of 20°N and west of 60°W that are not defined in the Gulf of Mexico; Bay of Biscay = bounded by 40°N and 20°W; West of Gibraltar = bounded by 20°W and between 25°N and 40°N; Mediterranean Sea = east of the Strait of Gibraltar; other areas = include all those areas in the northern latitudes that are not previously defined here.

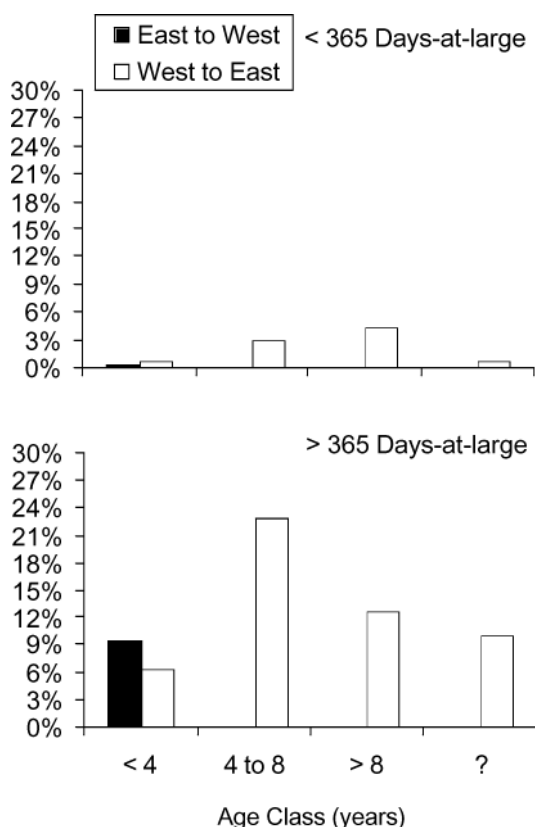


Figure 6. Relative recapture rates from conventional tagging for individual Atlantic bluefin tuna (*Thunnus thynnus*) crossing the management boundary (45°W longitude). The fish were assigned to age classes in accordance with their sizes at release and are designated according to Fromentin (2001): <4 (juvenile in the east or west), 4 to 8 (juvenile in the west or adult in the east), >8 (adult in west or east), ? (no size data were available). This graph is based upon the ICCAT tagging database, from which we eliminated records that were obvious duplicates. Some suspected duplicate records remained and therefore numbers reported here should be considered provisional until ICCAT determines the official status of records marked as suspected duplicates. Total number of recaptures from the western Atlantic was 4,716 (out of 42,485 releases), and from eastern Atlantic was 456 (out of 14,951 releases).

<1 year showed that there is little exchange between the eastern and western Atlantic, with less than 1% of recaptures in the Gulf of Mexico or western Atlantic (Table 2). Trans-Atlantic mixing rates were greater for individuals at large more than one year, with approximately 10% of juveniles recaptured in the western Atlantic along the U.S. and Canadian coasts. This estimate of east-to-west exchange is twice the rate (4.3%) reported by Fromentin (2001), and increased exchange appears more plausible since these estimates are not biased by shorter term (<1 yr) deployments. No individuals tagged in the eastern Atlantic were recaptured in the Gulf of Mexico, which is not surprising given the fact that these adolescents are not expected to occur on spawning grounds in the western Atlantic (Nemerson et al., 2000). Due to the small number of releases of individuals age 4 or older, conventional tagging data has provided little insight on the movement patterns of these

older age categories. Tagging data for fished released in the eastern Atlantic also indicate significant exchange of juveniles (<4 years) between the Mediterranean Sea and the eastern Atlantic, and this is consistent with the results of other studies that have suggested that large numbers of juvenile *T. thynnus* in the eastern Atlantic and in the Bay of Biscay result from the migration of juveniles from nursery areas within the Mediterranean Sea (Rodríguez-Roda, 1964b, 1969; Crespo and Rey, 1976; Rey and Cort, 1986; Cort and Liorzou, 1991; Cort and de la Serna, 1994; Cort and Liorzou, 1995; de la Serna et al., 2001; Rodríguez-Marín et al., 2005).

When the data are compared with respect to the two-stock premise, the relative importance of movement across the management boundary is quite different between shorter (<1 yr) and longer (>1 yr) times at liberty. Clearly, times at liberty of less than one year do not effectively characterize movement patterns, and the inclusion of these data into assessment models artificially reduces the degree of mixing across the management boundary; 0.7 to 4.2% for individuals at large <1 year and 6.3 to 22.8% for individuals at large >1 year (Table 2). In addition, the tendency for crossing the 45°W management boundary appears to be age dependent with a greater percentage of *T. thynnus* more than 4 years old showing this behavior. Unfortunately, only a small number of age 4–8 or > age 8 *T. thynnus* were tagged in the eastern Atlantic; thus data are insufficient to characterize east to west movement of older individuals. There are other potential problems that minimize the use of the conventional tagging database. In particular, reporting rates likely vary between the eastern and western Atlantic (and also among age/size classes). Punt and Butterworth (1995) provide indirect evidence that reporting rates are greater for fish recaptured in the western Atlantic than the eastern Atlantic, which may lead to underestimates of west to east movement. Finally, fishery removals will deflate the probability of detecting trans-Atlantic migrations as fish are removed prior to or during migrations. Given these biases, then qualitatively these data suggest that a small, but significant, proportion of *T. thynnus* from the western Atlantic migrate to the eastern Atlantic and further, that a small but significant portion of school-size fish in the western Atlantic may originate from spawning in the Mediterranean Sea (Figure 6). Thus, west to east migrations must be interpreted with care as some fish represent migrants who are returning to their natal spawning ground. Before alternative explanations for the pattern of recaptures can be eliminated, work must be conducted to understand how reporting rates and probability of recapture vary with area, time of year, and fish age/size.

3.2. Electronic Tagging

Recent advances in electronic tagging technologies for marine fish have provided scientists with new methods to document the movement and stock structure of *T. thynnus* (Arnold and Dewar, 2001; Gunn and Block, 2001). Historically, efforts to understand stock structure and population dynamics have been hampered by the inability to track movements of highly migratory fish over long durations. For example, conventional tags provide valuable data on a range of life history parameters, but their utility is limited in studies of movements by the lack of information on locations between release and recapture. Alternatively, electronic tags record ambient light level, water and/or body temperature, and pressure at frequent intervals throughout the deployment duration, which allows for estimation of position in association with diving behavior and thermal physiology (Teo et al., 2004; Block et al., 2005). In addition, temperature and depth data recorded by these electronic tags also provide insight into preferred habitat, foraging ecology, and thermal and reproductive biology of *T. thynnus*.

Armed with these new tools, researchers in both the east and west have used electronic tags to study the movement and stock structure of *T. thynnus* (e.g., Block et al., 1998a, 1998b, 2001a, 2001b, 2005; Lutcavage et al., 1999; De Metrio et al., 2002; Wilson et al., 2005; Stokesbury et al., 2004; Sibert et al., 2006; Teo et al., 2007).

The Tag-A-Giant (TAG) Program, a collaboration of Stanford University, the Monterey Bay Aquarium, and NOAA, was the first to deploy electronic tags on *T. thynnus* (Block et al., 1998a, 2001b; Gunn and Block, 2001). As of January 2006, TAG scientists had deployed 913 electronic tags of which 323 were pop-up archival transmitting (PAT) tags and 590 were implantable archival (IA) tags. Individual *T. thynnus* tagged by the program have ranged in size from 138 to 268 cm CFL (average size 190 to 230 cm CFL), and tracks of up to 4.8 years have been obtained. The majority of tags have been deployed off North Carolina (NC, $n = 829$), with smaller numbers of deployments in waters off New England and Canada ($n = 33$), the Gulf of Mexico ($n = 42$), and the west coast of Ireland ($n = 6$). TAG scientists have also collaborated on the deployment of tags in the Mediterranean basin (De Metrio et al., 2002). To date, 260 PAT tags have transmitted data and 13 of these have been recovered. In addition, 107 IA tags have been recovered in the western Atlantic ($n = 63$), eastern Atlantic ($n = 13$), and Mediterranean Sea ($n = 31$). Over 16,000 days of data on the movements and diving behavior of *T. thynnus* have been collected from IA and PAT tags by TAG (Block et al., 1998a, 2001b, 2005; Gunn and Block, 2001; Teo et al., 2004; Stokesbury et al., 2004; Teo et al., 2007). The location estimates obtained from the light data indicate that on average, *T. thynnus* moved from 1.6 to 71.6 km/day (average = 16.2 ± 2) with a maximum distance traveled of 5820 km in 304 days.

Block et al. (2001a, 2005) summarized movement data collected on *T. thynnus* using IA and PAT tags from the TAG Program from 1996 to 2004. They describe distinct patterns of *T. thynnus* distribution associated with ontogeny, seasonal shifts, and fidelity to natal spawning ground. Individuals tracked for less than one year showed high residency in the western Atlantic, moving between winter grounds off the south Atlantic states into northern waters of the Gulf of Maine. Individuals less than 200 cm CFL moved north or northeast in the late winter or early spring, with most fish moving into New England waters, occupying areas overlying the continental shelf. None of these fish entered a known spawning ground and most remained west of 45°W. The following winter the fish returned to North Carolina. Conversely, older *T. thynnus* (>200 cm CFL) visited spawning grounds in the Gulf of Mexico or Mediterranean Sea, although no individual visited both spawning areas during the tracking period. Five individuals showed fidelity up to three consecutive years to either the Gulf of Mexico or the Mediterranean Sea spawning ground. Trans-Atlantic migration of western-tagged *T. thynnus* into the Mediterranean occurred for 23 individuals. Several *T. thynnus* tagged in the western Atlantic moved into the highly productive waters east of the central North Atlantic to the east of the Flemish Cap or west of the Iberian Peninsula.

To examine mixing and spawning site fidelity, Block et al. (2005) categorized *T. thynnus* by their visitation to a known spawning ground. Individuals that visited known spawning grounds in the western Atlantic during the spawning season and occupied water temperatures >24°C for seven days were characterized as western spawners ($n = 36$). Those that were either in the Mediterranean Sea or were apparently in transit to or from the spawning grounds during the spawning season were considered to be eastern Atlantic spawners ($n = 23$, plus 3 recaptures). While most IA and PAT tagged *T. thynnus* categorized as western spawners traveled to the Gulf of Mexico, some also went to either the Bahamas ($n = 6$) or the northern Caribbean ($n = 1$). Individuals that visited no spawning ground were considered neutral (81% of recovered IA or PAT tags; $n = 268$). Geolocation estimates for all *T. thynnus*

classified as eastern or western spawners indicated there was substantial mixing along the eastern seaboard of the United States and in the central North Atlantic foraging grounds (Figure 7). Importantly, there was no evidence for mixing on the spawning grounds in the Gulf of Mexico or the Mediterranean Sea, supporting the two-stock hypothesis.

The probability of residency within the western Atlantic management unit was also estimated for eastern and western Atlantic spawners in defined blocks of time at large (0–180 days, 180–360 days, 360–720 days, and >720 days) to account for differences in track length (Block et al., 2005). Values reported here encompass the 95% confidence limits. For an individual identified as a western Atlantic spawner, the probability of staying within the western Atlantic management zone was high over all track duration intervals, ranging from 84% to 100%. For the eastern Atlantic spawners, the probability of utilizing the western Atlantic decreased steadily with time from a maximum of 93% for 1–180 days at large to 5% after 720 days. This suggests that after 720 days almost all *T. thynnus* identified as eastern Atlantic spawners had returned to the Mediterranean Sea and remained in the eastern Atlantic. For neutral fish, the probability of occurring in the west decreased slightly from a maximum of 99% for 1–180 days at large to a minimum of 86% for fish at large >720 days. These data indicate that track duration (short tracks bias the fish to the western

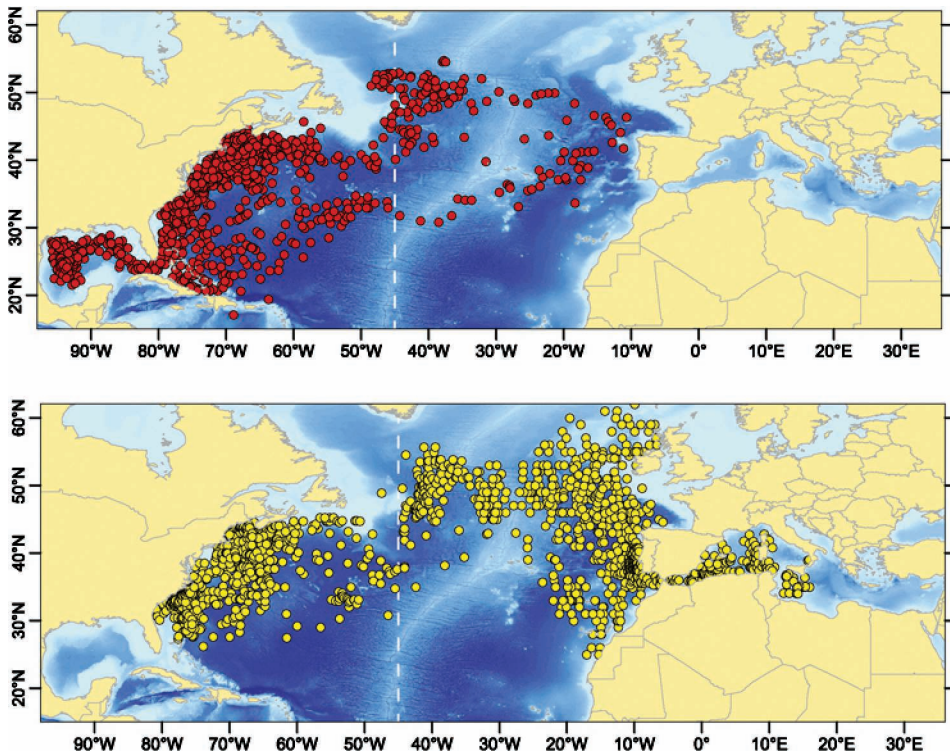


Figure 7. Geolocation estimates of Atlantic bluefin tuna (*Thunnus thynnus*) from the Tag-A-Giant Program. Daily geolocation (from light level longitude and SST-based latitude) or deployment/pop up locations are shown *T. thynnus* classified as western ($n = 36$) or eastern ($n = 26$) spawners. Data provide information on movements that reveal two populations of *T. thynnus* in the North Atlantic that share common foraging grounds as adolescent and adults but sort to western breeding grounds (red circles) and the Mediterranean Sea (yellow circles). Data from Block et al. (2005).

Atlantic) and origin can be used to predict the probability of an individual being in a specific management zone.

The PAT and IA tag data also provided insight into the reproductive age for the eastern Atlantic *T. thynnus*. In the east, *T. thynnus* displaying trans-Atlantic migrations into the Mediterranean Sea (average size at release 207 cm \pm 17 CFL or 8.6 years of age) remained in the western Atlantic for 0.5 to 3 years prior to traveling to the eastern Atlantic or Mediterranean. The observation that individuals spawned at much greater sizes and ages than currently assumed for the eastern Atlantic stock after at least one year of no spawning suggests that a contingent of *T. thynnus* matures substantially later than those typically sampled on the Mediterranean Sea spawning ground (Block et al., 2005).

Three individual *T. thynnus* with long records (3.3 to 4.6 years) showed spawning site fidelity to the Mediterranean Sea, returning to spawning grounds in consecutive years. Once eastern Atlantic spawners entered the Mediterranean Sea, they did not subsequently move westward across the 45°W meridian (Figure 8). Instead, these individuals preferentially foraged along the western European coastline and extended their range into coastal waters off Ireland. Results indicate that a portion of the eastern Atlantic stock recruits as adolescent tunas into the western Atlantic fishery and forages along the continental shelf. Once the fish approach sexual maturity (again at presumably much older ages than expected for the population), they return to the Mediterranean Sea and remain within the eastern management zone for the duration of their tracks (up to 4 years), with no evidence of a return trip to the western Atlantic. Spawning site fidelity was also noted, with two individuals classified as western Atlantic spawners making consecutive trips for two or three years back into the Gulf of Mexico in the spring.

Researchers from the Large Pelagics Research Center (LPRC) at the University of New Hampshire have also used electronic tags to follow the movements of *T. thynnus* in the western Atlantic. Lutcavage et al. (1999) deployed PAT tags on *T. thynnus* caught off New England (estimated length: 190 to 263 cm SFL). Data were received from 17 of the 20 tags deployed, all of which were in the central Atlantic, including those that released during the purported spawning period in the Gulf of Mexico and Mediterranean Sea. This led the authors to hypothesize that spawning may occur in the mid-Atlantic. However, results of Block et al. (2005) and Diaz and Turner (2006) suggest that *T. thynnus* of the western Atlantic spawn first spawn at about 11 years of age, so it is possible that many of the fish tagged by Lutcavage et al. (1999) were not mature. Also, early generation PAT tags lacked the capacity to detect premature release, making the estimation of the period of attachment on long deployments difficult to assess (Stokesbury et al. 2004). In later studies by the LPRC, 68 PAT tags were deployed on *T. thynnus* estimated to be from 91 to 295 kg (average 201 cm SFL) (Wilson et al., 2005). Most tags (67) were deployed in the Gulf of Maine with one tag deployed off North Carolina. The time at large for these individuals ranged from 6 to 304 days (average 115 \pm 90 days). Again, none of the fish visited known spawning grounds during their tracks, which is possibly due to the fact that many of them may have been immature and they were at large for only short periods.

Tagging campaigns using electronic tags have also been initiated in the Mediterranean Sea over the last decade (De Metrio et al., 2002, 2004). De Metrio et al. (2005) summarized PAT tags released from 1998–2004 in three tagging regions in the Mediterranean Sea: eastern Mediterranean (Levantine Sea), central Mediterranean (Tyrrhenian Sea off Corsica and Sardinia), and western Mediterranean Sea (Strait of Gibraltar to eastern Atlantic). No evidence of trans-Atlantic migration was detected; however, longer deployment periods are often necessary to determine the potential for trans-Atlantic migration. Movement of *T. thynnus* tagged within the Mediterranean Sea was often limited, particularly for individuals

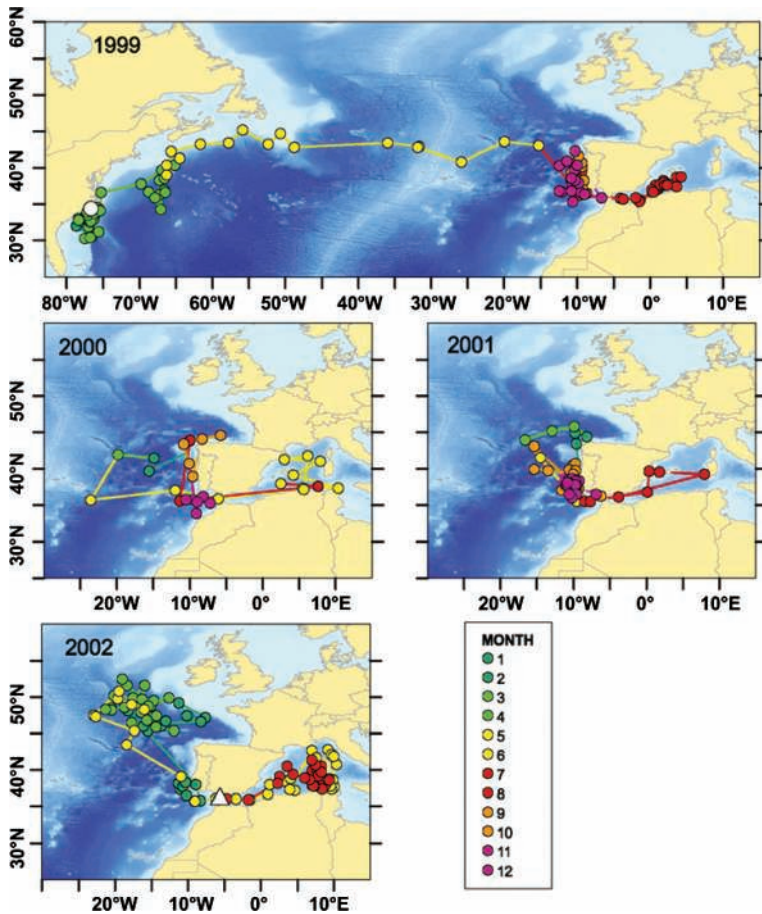


Figure 8. Movement of an individual Atlantic bluefin tuna (*Thunnus thynnus*) tagged in the western Atlantic that showed spawning site fidelity to the Mediterranean Sea (222 cm CFL at tagging, 1999–2002). 1999, Archival tag 705 was deployed off North Carolina on 11 February 1999. In the first year of the track, the fish migrated from the North American shelf waters to the Mediterranean spawning areas. 2000–2002, It spent the next three years (2000–2002) in the eastern Atlantic, visiting Mediterranean putative spawning areas in each year and was recaptured in the Strait of Gibraltar on 31 August 2003 (white triangle). Daily latitude estimates for the first year were made using SSTs¹⁰, up to when the temperature sensor broke (7 October 2001). Subsequent daily latitude estimates were made using light levels. Daily calculated geolocations are color coded by month (see legend).

tagged in the central or eastern regions of the basin (Figure 9). Also, of the PAT tags deployed in the eastern Mediterranean Sea, all pop-up locations were in areas very close to the release site, with a few individuals located in the Aegean Sea or in areas not far from the North African coast in the eastern basin of the Mediterranean Sea. Yamashita and Miyabe (2001) also reported that young *T. thynnus* tagged with archival tags in the Adriatic Sea remained close to the deployment area within the Mediterranean. Movement of *T. thynnus* tagged in the central and western Mediterranean Sea was more pronounced than in the east, particularly for individuals tagged in the western region. Several individuals moved west of the Strait of Gibraltar, with two individuals moving several thousand kilometers to

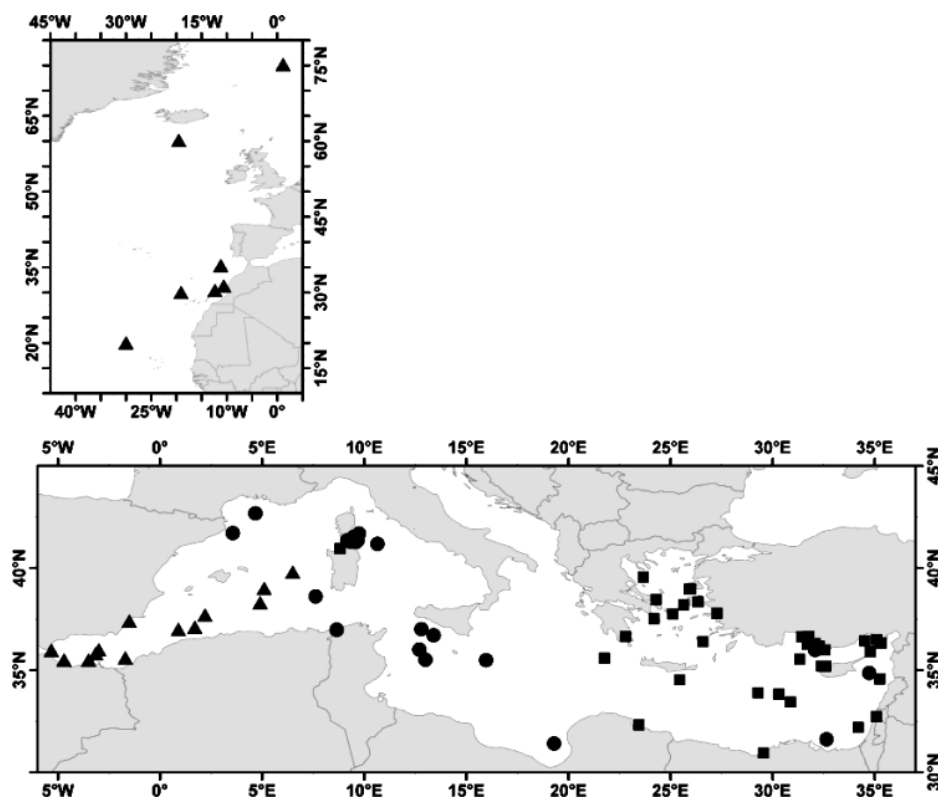


Figure 9. Positions of pop-up satellite archival tags from Atlantic bluefin tuna (*Thunnus thynnus*) deployed in the Mediterranean Sea and eastern Atlantic during 1998–2004. Symbol shapes denoted deployment location in Mediterranean: eastern (square), central (circle), western Mediterranean and eastern Atlantic close to Strait of Gibraltar (triangle). Based on data from De Metrio et al. (2005).

the north in the general vicinity of Iceland (Figure 9). De Metrio et al. (2005) suggested that movement patterns or displacement distance was linked to size, with larger individuals (>150 kg) being more likely to move out of the Mediterranean, as previously hypothesized by Sarà (1964, 1973). More recently, Stokesbury et al. (2007) reported that giant *T. thynnus* tagged in the eastern Atlantic off Ireland moved from these areas across the 45°W stock boundary over short periods of time, demonstrating connectivity between eastern foraging grounds and western Atlantic fisheries.

3.3. Chemical Markers

Chemical markers in hard parts (otoliths, bone) represent a promising alternative to tagging or genetics studies for determining the movement and stock structure of *T. thynnus*. The principal assumption underlying the approach is that hard parts precipitate material as the tuna grows and the chemical composition of the otolith or bone is linked to the composition and/or physicochemical conditions of the water mass they inhabit (Calaprice, 1986; Campana, 1999; Thresher, 1999; Rooker et al., 2001a). Therefore, material deposited in the otolith or bone during the first year of life serves as a natural indicator of an individual's nursery habitat or origin. Elemental signatures in the vertebrae of *T. thynnus* were first described by Calaprice (1986), who used the technique to discriminate individuals from the eastern and western Atlantic. The validity of the approach was further confirmed by studies

Table 3

Chemical signatures (mean and ± 1 SE) in the whole otoliths of age-0 and age-1 Atlantic bluefin tuna (*Thunnus thynnus*) from the western Atlantic and eastern Atlantic/Mediterranean Sea

	W. Atlantic		Mediterranean	
	Mean	SE	Mean	SE
Li	0.216	0.020	0.250	0.008
Mg	36.998	3.331	33.979	0.527
Mn	2.851	1.256	1.111	0.050
Sr	1095.450	75.350	1119.279	15.287
Ba	0.765	0.064	0.747	0.020
Li	0.140	0.004	0.222	0.015
Mg	19.642	0.877	25.205	0.952
Mn	0.618	0.034	0.782	0.076
Sr	1394.081	14.090	1301.290	38.011
Ba	1.300	0.039	1.134	0.071
$\delta^{13}\text{C}$	-8.313	0.056	-8.845	0.043
$\delta^{18}\text{O}$	-2.089	0.055	-1.029	0.260

Elements: age-0 ($n = 59$ east, $n = 2$ west); age-1 ($n = 42$ east, $n = 29$ west); Stable isotopes: age-1 ($n = 93$ east, $n = 37$ west); Data source: Rooker et al., 2003, 2004, 2006a; Secor et al., 2002; J.R. Rooker unpublished data.

conducted on both Atlantic and Pacific bluefin tuna (Secor and Zdanowicz, 1998; Rooker et al., 2001a). Rooker et al. (2001b) measured six elements (Li, Mg, Ca, Mn, Sr, Ba) in the otoliths of juvenile *T. orientalis* and showed a clear separation in elemental signatures of juveniles from the Pacific Ocean and marginal sea nurseries. Similar studies have been conducted in the Atlantic for juvenile *T. thynnus* (age 0 and age 1) and differences in the concentrations of certain elements (Li, Mg, Mn) were detected between eastern and western Atlantic nurseries (Table 3; Secor et al., 2002; Rooker et al., 2003). However, classification success for several year-classes from these studies was moderate, ranging from 60 to 90%, and classification functions showed strong year-to-year variability, despite the fact that regional nurseries within the Mediterranean (Alboran Sea, Ligurian Sea, Tyrrhenian Sea) showed distinct differences that were relatively stable over time.

The utility of alternative geochemical markers in otoliths have been examined recently, and findings indicate that stable isotopes in otoliths ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) of *T. thynnus* can be used to effectively distinguish individuals from eastern and western nurseries (Rooker and Secor, 2004). Stable $\delta^{18}\text{O}$ signatures in otoliths of yearlings from each nursery were distinct, with enriched $\delta^{18}\text{O}$ values observed for *T. thynnus* from the cooler, more evaporative Mediterranean basin relative to the western Atlantic (Table 3), which is in agreement with global ocean records of Seawater $\delta^{18}\text{O}$ (Schmidt et al., 1999). Rooker and Secor (2004) demonstrated that the discriminatory power of stable isotopes in otoliths of yearling *T. thynnus* was high, with well over 90% of individuals classified correctly to eastern and western Atlantic nurseries (based on cross-validated classification from discriminant function analysis). In a followup study, Rooker et al. (2006a) compared otolith core material (corresponding to the first year of life) of large school, medium, and giant category *T. thynnus* collected in both the western Atlantic and the Mediterranean Sea to yearling signatures to determine their origin. Results from this preliminary assessment indicated that a large fraction (>50%) of

the adolescent *T. thynnus* collected in the western Atlantic fishery (comprised primarily of large school and medium category fish) originated from nurseries in the Mediterranean Sea, suggesting that catches in the western Atlantic are comprised in part of *T. thynnus* produced from spawning areas in the Mediterranean Sea. Alternatively, adult category *T. thynnus* collected in the Mediterranean Sea were almost entirely of eastern Atlantic origin (>90%), indicating strong natal homing to spawning/nursery grounds in the Mediterranean Sea.

3.4. Genetics

Attempts to test the two-stock hypothesis of stock structure were initially based on allozyme variability, which showed no evidence of population subdivision (Edmunds and Sammons, 1971, 1973; Thompson and Contin, 1980). In general, allozyme markers revealed very low levels of diversity in *T. thynnus*, with an average heterozygosity of $H = 0.029 \pm 0.019$ for 37 loci surveyed (Pujolar et al., 2003). In addition, some polymorphisms displayed by certain enzymes have been attributed to artifacts. For instance, genetic heterogeneity associated with *G6PDH** (Phipps, 1980, Pujolar et al., 2001) is suspect because the scoring of this locus is unreliable (Pujolar et al., 2003), and perhaps a function of tissue quality (Thompson and Contin, 1980). Similarly, the temporal heterogeneity at *SOD2** reported between spring and fall samples collected in St. Margaret's Bay, Canada, was suggested to be the result of the presence of null alleles at this locus (Phipps, 1980). The only study using allozymes suggesting heterogeneity between eastern and western Atlantic was based on pooled Mediterranean/eastern Atlantic ($n = 738$) and western Atlantic ($n = 39$), yielding a significant differentiation at *SOD-1** ($P = 0.002$), with a regional inversion of allele frequencies at this locus (Pujolar et al., 2003). However, since the multilocus P -value for all 37 loci was not significant, the authors concluded that no differences exist between eastern and western stocks of *T. thynnus*.

In contrast with the low levels of variability revealed by allozymes, the characterization of *T. thynnus* mtDNA control region (CR)-I sequences by Alvarado Bremer et al. (1999) revealed substantial amounts of genetic variation ($h = 0.99$) and provided the first evidence of population subdivision between the western Atlantic ($n = 67$) and the Mediterranean Sea ($n = 73$) ($\Phi_{st} = 0.0119$; $P = 0.0270$). Still, when additional samples were characterized, the reported mtDNA difference between the east and west was no longer evident (Ely et al., 2002). This result was later supported by a more extensive comparison of samples from the western Atlantic ($n = 141$) and the Mediterranean Sea ($n = 436$) (Alvarado Bremer et al., 2005; $\Phi_{st} = 0.002$, $P = 0.245$). In contrast, Carlsson et al. (2004) reported significant heterogeneity among three regions within the Mediterranean Sea with mtDNA CR sequence data ($\Phi_{st} = 0.0233$, $P = 0.000$), and also with the allele frequencies from nine microsatellite loci ($F_{st} = 0.0023$, $P = 0.038$). The signal of differentiation was primarily associated to the difference between an eastern Mediterranean sample from the Ionian Sea and a western Mediterranean sample from the Tyrrhenian Sea. Although their Ionian sample was not different from another western Mediterranean sample, the Balearic Sea, the authors suggested that a discrete population of *T. thynnus* may reside in the eastern Mediterranean. Because of the large number of alleles often associated with microsatellite loci, comparative surveys require large sample sizes to distinguish true signals of stock structure from sampling artifacts (DeWoody and Avise, 2000). In addition, the analysis of microsatellite loci in fish with large populations and high gene flow appears to be confounded by allele size homoplasy which tends to result in underestimates of genetic differentiation (O'Reilly et al., 2004). This may explain the results of Broughton and Gold (1997) using

microsatellites who reported the genetic differentiation of a small western Mediterranean sample ($n = 12$) against several eastern Mediterranean samples of *T. thynnus*, but not against a sample of *T. orientalis*. Since size homoplasy appears to correlate directly with mutation rate, it is advisable to avoid highly polymorphic microsatellite loci in stock structure studies (O'Reilly et al., 2004). Clark et al. (2004) developed an additional 25 microsatellite loci for *T. thynnus* that could be screened to further test hypotheses of stock structure (see also Tagaki et al., 1999; McDowell et al., 2002), as well as to provide estimates of effective population sizes which may also serve as criteria to identify population subdivision (J. Gold, personal communication; Carlsson et al., 2004).

One of the major shortcomings of previous genetic studies was that samples of *T. thynnus* used to represent the “western stock” were collected along the eastern seaboard of the United States, where mixing of the two stocks occurs (Block et al., 2005; Rooker et al., 2006a), and not from the Gulf of Mexico spawning ground. This limitation has been avoided in recent studies by including samples of larvae or adults from spawning grounds in the Gulf of Mexico and Mediterranean Sea. Carlsson et al. (2007) examined YOY *T. thynnus* collected from spawning grounds in the Gulf of Mexico and the Mediterranean Sea and detected statistically significant differentiation at 8 nuclear microsatellite loci ($F_{ST} = 0.0059$, $p < 0.001$). Moreover, the global Φ_{ST} at mtDNA control region sequences was significantly different from zero ($\Phi_{ST} = 0.0129$, $P = 0.014$) between YOY from the two regions. The authors also noted the presence of “albacore-like” mtDNA in YOY *T. thynnus* from the Mediterranean Sea (frequency $\sim 5\%$) but not in individuals from the Gulf of Mexico. These “albacore-like” mtDNAs actually include “*T. orientalis*-like” mtDNA (frequency $\sim 2\%$), and introgressed *T. alalunga* mtDNA (frequency $\sim 3\%$) in addition to other “rare” types (Figure 10). Boustany et al. (2006) also examined mtDNA sequences of adult *T. thynnus* from spawning grounds in the Gulf of Mexico ($n = 55$) and Mediterranean Sea ($n = 105$) and found significant divergence between the two regions ($\Phi_{ST} = 0.0110$, $p = 0.041$), with a high overall haplotype diversity (0.9861 ± 0.0053). Nearest neighbor and AMOVA analyses also suggested that individuals from the Gulf of Mexico and Mediterranean Sea were distinct. Similarly to above, the authors reported that the absence of “*T. orientalis*-like” and “*T. alalunga*-like” mtDNAs from adults on spawning grounds in the Gulf of Mexico (Boustany et al., 2006). Although results from these studies need to be corroborated with additional samples from several year classes to verify the stability of the reported signals, findings from both studies support the hypothesis of some genetic isolation between *T. thynnus* from the Gulf of Mexico and Mediterranean Sea and are consistent with the natal homing behaviors observed from archival tagging studies.

As discussed previously in this review, evidence of mixing between the eastern and western Atlantic is well documented from conventional tagging, IA and PAT tagging, and otolith chemistry. If constant mixing between of *T. thynnus* from the east and west occurs, even at low levels ($\approx 2\%$), then any genetic signal of differentiation is expected to be extremely weak, requiring the comparison of large sample sizes to have sufficient statistical power (Waples, 1998). It should be noted that mixing might not necessarily translate into gene flow, as long as philopatric behavior towards separate breeding areas is maintained, as documented earlier in this review. Also, the weak signal of genetic differentiation that separates the eastern and the western Atlantic stocks may be associated to a relatively recent population expansion in the Atlantic, followed by the re-colonization of the Mediterranean after the last glacial maximum. Under this scenario, even if the two stocks were completely isolated from each other, not enough time would have lapsed for lineage sorting to occur (Alvarado Bremer et al., 2005).

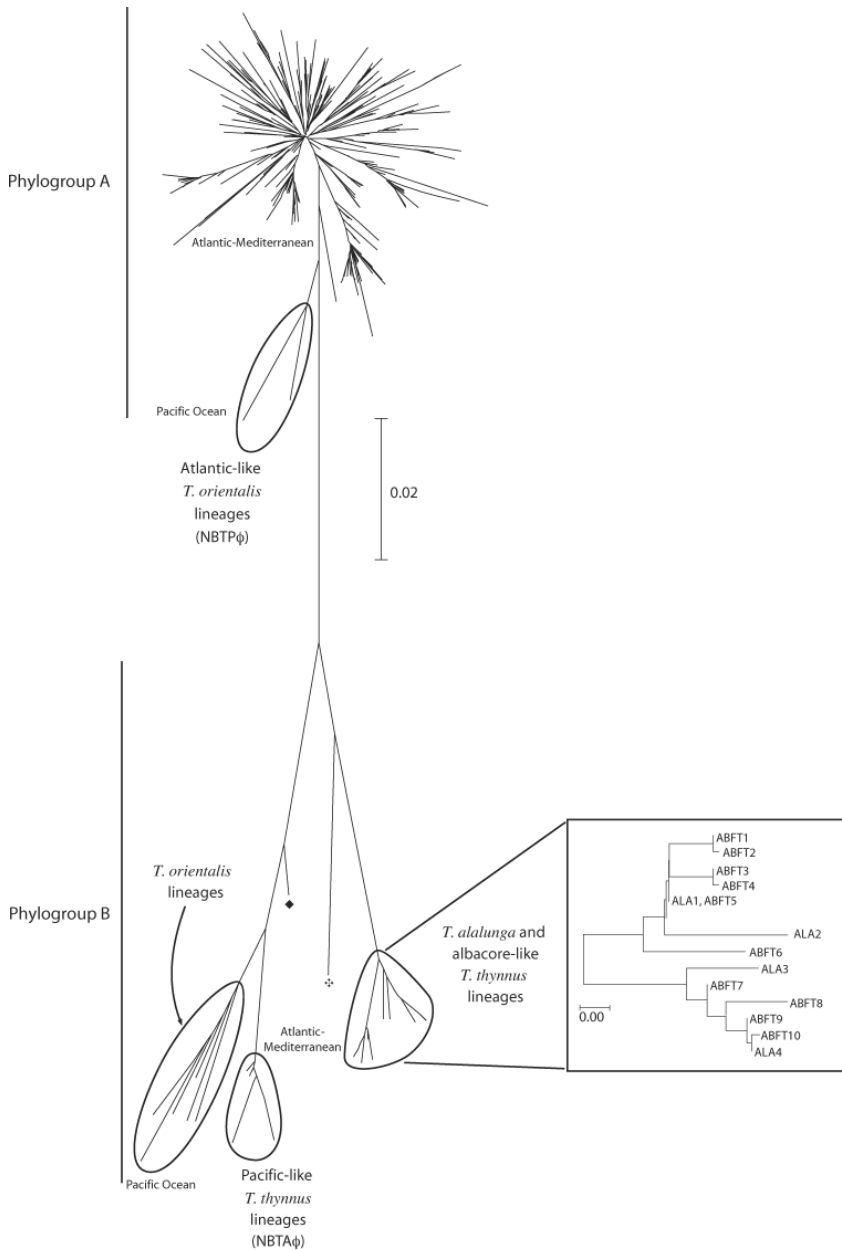


Figure 10. Neighbor joining depicting the complex phylogenetic signal of *T. thynnus* mtDNA that includes “*T. orientalis*-like” and introgressed *T. alalunga* lineages (modified from Alvarado Bremer et al., 2005). The majority of *T. thynnus* (frequency $\sim 95\%$) belong to Phylogroup A, a group that also includes rare Atlantic-like *T. orientalis* (NBTP ϕ) lineages. The remaining 5% of *T. thynnus* are more closely related either to *T. orientalis* or to *T. alalunga* and collectively they form Phylogroup B. Accordingly, about 2% of *T. thynnus* haplotypes correspond to the Pacific-like *T. thynnus* (NBTA ϕ), whereas the remaining 3%, identified in the inset with the acronym (ABTn), correspond to introgressed *T. alalunga* mtDNA. Phylogroup B also contains two relict *T. thynnus* haplotypes. The first (\blacktriangle) is sister to *T. orientalis* + Pac-like *T. thynnus*, and the second (\blacklozenge) is sister to *T. alalunga* and albacore-like *T. thynnus* lineages. The tree was rooted at mid-point and was based on CR-I sequences.

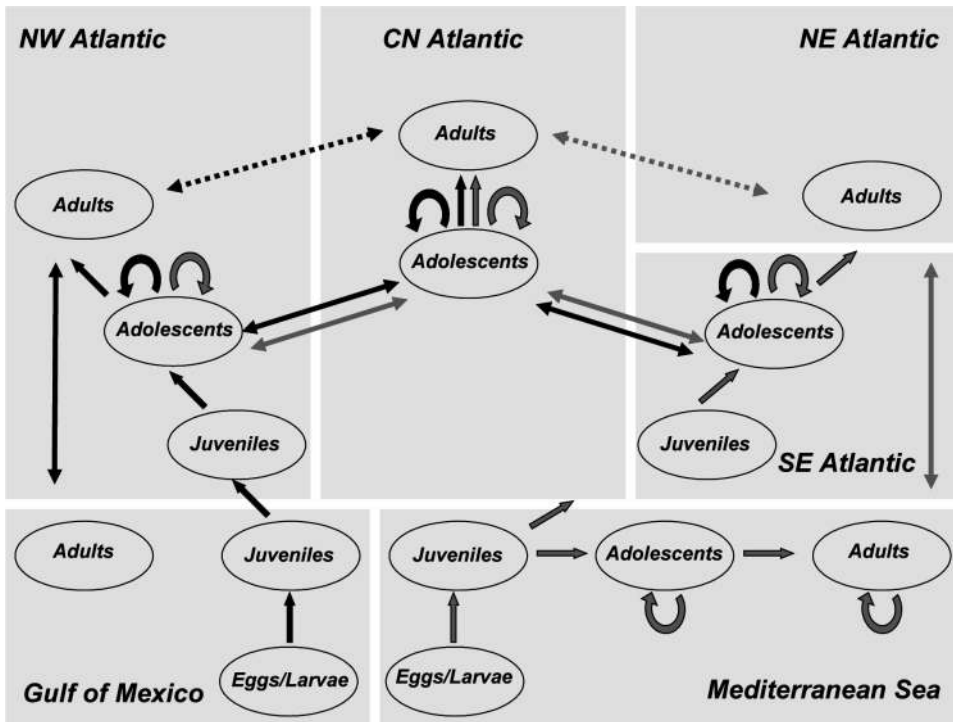


Figure 11. Life history cycles of the eastern and western Atlantic bluefin tuna (*Thunnus thynnus*) populations based on the two-stock, six-zone management regime.

3.5. Mixing and Management

Results of recent studies on *T. thynnus* support two fundamental premises: (1) there are two principal spawning regions and associated populations contributing to *T. thynnus* fisheries, and (2) these stocks intermingle across the North Atlantic basin in a complex but structured manner (Figure 11). Electronic tagging data in particular have provided fascinating insights into the complex oceanography and phenotypic modalities that underlie migration pathways of *T. thynnus*, while genetic evidence and otolith chemistry both support classification of individuals into two groups based upon genetic lineages and nursery of origin. Nemerson et al.'s (2000) failure to find evidence for adults less than 190 cm CFL on the Gulf of Mexico spawning grounds is supported by similar results from Block et al. (2005) and Diaz and Turner (2006), indicating that there is strong evidence for fundamental life history differences between the two stocks, consistent with current views on maturity schedules (Figure 3).

The intermingling of stocks has two important consequences in managing for sustainability: (1) the western Atlantic stock is disproportionately affected by migrants that contribute to eastern Atlantic and Mediterranean fisheries, and (2) western Atlantic fisheries currently (and presumably historically) depend upon migrants from the eastern Atlantic to a greater degree than the converse case. The effect of mixed stocks fisheries on sustainability is dependent upon the product of each constituent population's exchange rate and productivity level. Because the eastern Atlantic stock's productivity is estimated to be at least 10-fold that of the western Atlantic stock (Fromentin and Powers, 2005), even large (several-fold)

differences in exchange rates are unlikely to affect these two consequences. Further, these consequences are consistent with the lack of recovery for the western stock despite stringent regulatory measures and evidence for high subsidization of western Atlantic fisheries by *T. thynnus* of Mediterranean origin (Rooker et al., 2006a).

The existence of structured migration pathways, evident from electronic tagging information (Block et al., 2001a, 2005), suggest that spatially explicit regulation strategies might be effective in building sustainable interjurisdictional fisheries for *T. thynnus*. Most immediately, it is apparent that the central North Atlantic comprises an important foraging ground for western-origin juveniles and adults. Although we do not yet know the relative composition of eastern and western stocks on the central North Atlantic foraging ground, we might expect that fisheries in this region would have a larger effect on the western stock than fisheries in the Mediterranean, where there are fewer individuals of western origin. Thus, imposing regulations in the central North Atlantic that are related to western stock rebuilding thresholds rather than eastern stock fishery thresholds would seem prudent. Alternatively, area closures may be effective when information on mixing is too uncertain to guide informed regulations.

The priority for more integrated and spatially explicit management of *T. thynnus* has stimulated ICCAT to form a special working group to develop alternatives to the two-stock (two-zone) management regime. In 2001, SCRS proposed a six-box model with the regions being the Gulf of Mexico, Western Atlantic, Central North Atlantic, Northeastern Atlantic, Eastern Atlantic, and Mediterranean Sea (Figure 11). This model, a two-stock, six-zone management regime, which matches more accurately the known life cycles of the two stocks, would permit regulations more tailored to mixing rates that could be estimated through otolith chemistry or genetic methods. Secor (2002) and Fromentin and Powers (2005) emphasized that contingent structure within stocks could support more resolved spatial management, where contingents represent intrapopulation groups of individuals that engage in similar life-time migration patterns. The group of late-maturing *T. thynnus* of Mediterranean origin described by Block et al. (2005) probably represents such a contingent. Therefore, contingents and their behaviors can be identified through the combined use of electronic tagging and otolith chemistry. If such behaviors can be generalized, then spatially explicit management across several zones would become feasible. Alternatively, because exchange rates vary with fish size (e.g., juveniles of western origin are more likely than adults to be recaptured in the Mediterranean), shifting fishery selectivity patterns (in this example from juveniles toward adults) could also be an effective means to reduce the effect of mixing on fisheries sustainability.

4. Summary and Recommendations

Recent findings from several types of investigations have increased our knowledge of *T. thynnus* life history and stock composition. In particular, our understanding of reproduction, foraging, migration, and stock structure has increased profoundly in the last decade, with much of this linked to the development and application of novel tools, including dietary tracers, IA and PAT tags, otolith chemistry, and molecular markers. In addition, insights from conventional approaches and meta-analytical interpretation of existing data sets have helped to clarify various aspects of *T. thynnus* biology. Key aspects of the stock structure of *T. thynnus* that have been determined or clarified with some degree of certainty over the past decade are described below.

1. Two primary spawning stocks exist with spawning areas located in the Gulf of Mexico and Mediterranean Sea. Regional variation within each spawning area exists with multiple spawning locations present in both areas. Three distinct spawning areas are present in the Mediterranean Sea (southern Italy around Sicily, Balearic Archipelago off Spain, Levantine Sea), albeit other spawning areas may also occur within the basin. In the Gulf of Mexico, spawning occurs primarily in the northern slope waters between the 200- and 3000-m contours, particularly in waters west of Loop Current. Because the Loop Current varies in its location from year to year, so too does the distribution of eggs and larvae in the Gulf of Mexico. In both the Gulf of Mexico and Mediterranean Sea, the location and intensity of spawning is influenced by the spatial and temporal variability in the location of major oceanographic features (fronts) and environmental conditions (e.g., waters with sea-surface temperatures above the 24°C threshold).
2. The timing and distance traveled to spawning grounds varies among spawning adults with origins in the eastern and western Atlantic. In the western Atlantic, individuals make directed movements from foraging grounds in the western and central North Atlantic to the Gulf of Mexico in the late winter and early spring, with the most individuals present on the spawning grounds from March to early July. A fraction of the stock moves into highly productive waters of the Gulf of Maine, Scotian Shelf, central North Atlantic, east of the Flemish Cap, or west of the Iberian Peninsula before returning to the Gulf of Mexico to spawn. The central North Atlantic also serves as foraging grounds for members of the eastern stock, and movement out of the Mediterranean Sea to this region is well documented. A portion of the eastern Atlantic stock recruits as adolescents to the western Atlantic fishery and forages along the continental shelf of the United States. As these fish approach sexual maturity, they return to the Mediterranean Sea to spawn from June to August. Following their return to the Mediterranean Sea, evidence to date indicates they do not return to western foraging grounds. Site fidelity to natal areas occurs after the fish reach reproductive maturity. Thus, individuals are limited to either the eastern or western spawning ground, supporting the two-stock premise.
3. Fertility schedules of *T. thynnus* in the eastern and western Atlantic are markedly different, with individuals reaching sexual maturity as early as age 3 or 4 in the eastern Atlantic. In contrast, recent analyses based on length-frequency and electronic tagging data indicate that maturation of *T. thynnus* in the Gulf of Mexico begins much later (age 8), with the majority of individuals on the spawning grounds being 10 years of age or older (mean age about 11 years).
4. Both opportunistic foraging strategies and ontogenetic shifts in prey selection patterns are evident at major life history transitions. Foraging depth varies as a function of prey distribution with most individuals feeding in the upper mixed layer. Diets of juveniles and adults are comprised mainly of fishes, cephalopods, and euphausiid crustaceans, and foraging is not limited to the water column (demersal organisms constitute up to 20% of diet in shallow water areas). Tracer studies indicate that the trophic position of adult *T. thynnus* is one level higher than those of other congeners.
5. Growth among young fish (ages 1 to 5) does not vary significantly between eastern and western Atlantic stocks; however, growth trajectories for older individuals diverge, with size at age being greater for the western Atlantic stock. Sex-specific differences in growth occur, with males growing slightly faster than females and reaching slightly larger sizes by age 10. Although separate size-at-age models are currently used for ICCAT assessments, growth curves for the eastern and western Atlantic are based on different aging approaches, which may be problematic and warrants further attention. Recent research validating ages based upon bomb radiocarbon dating methods shows

promise and preliminary data from this analysis indicate that current models could be overestimating growth rate and underestimating longevity.

6. Trans-Atlantic mixing is significantly greater than indicated by earlier assessments, which were based on conventional tagging data. Data from conventional tags (for fish >1 year at liberty), electronic tags, and otolith chemistry suggest that a fraction of adolescents of Mediterranean origin are mixing with their western counterparts on foraging grounds along the eastern seaboard of the United States. Movement of western Atlantic *T. thynnus* into the central North Atlantic is of particular concern because it subjects these individuals to fisheries in the eastern Atlantic, for which fishing quotas are an order of magnitude higher. Assessing the degree of west to east movement for *T. thynnus* of western Atlantic origin versus individuals of eastern Atlantic origin is of critical importance to future assessments.
7. Movement and trans-Atlantic migration are age specific, and juvenile or adolescent *T. thynnus* from both the eastern and western Atlantic are highly mobile and commonly mix in different areas of the Atlantic Ocean. Since these individuals are reproductively immature, they are often on mixing grounds during presumed spawning periods. When these individuals reach reproductive maturity and begin frequenting spawning grounds in the Gulf of Mexico or Mediterranean Sea, trans-Atlantic mixing is less evident.
8. The stock structure is more complex than originally anticipated and appears to meet the criteria of a "patchy population" as described by Hanski and Gilpin (1991) because some fraction of the stock undertakes trans-Atlantic migration annually and/or ontogenetically but migrants return to their natal sites to spawn. Moreover, structuring within a basin or spawning ground has been observed in the Mediterranean Sea where the existence of a local or resident eastern Mediterranean subpopulation has been hypothesized. Recent findings from electronic tagging and genetic studies appear to lend credence to this theory (De Metrio et al. 2005). Clearly, any level of structuring between and within eastern and western Atlantic stocks will impact fishery yields and recovery efforts. Thus, the development of more complex models or management regimes that emphasize contingent structure within stocks (e.g., the SCRS two-stock, six-zone management model) will support more resolved spatial management and permit regulations more tailored to mixing rates that could be estimated through otolith chemistry or genetic methods.

Despite our improved understanding of *T. thynnus*, significant data gaps still exist and must be addressed to ensure recovery and optimal utilization. Promising results from novel approaches must be continued and expanded to provide managers with the necessary information to protect this resource. Recommendations for future research should include the following objectives:

1. Improve our current understanding of movement during the first year(s) of life. Similar to *T. orientalis*, trans-oceanic movement during the first few years may be important, and this issue warrants further attention. Fortunately, electronic tagging (sonic and archival implants) of juvenile *T. thynnus* began in 2005 by researchers in the eastern Atlantic (AZTI Tecnalia) and western Atlantic (LPRC "Tag-a-Tiny" Program), which should help elucidate migration paths of juveniles.
2. Define boundaries of the putative spawning and/or nursery grounds of *T. thynnus* in the Gulf of Mexico and Mediterranean Sea and areas outside these regions where larvae have been collected (e.g., Bahamas, Straits of Florida). To accomplish this objective, data from directed ichthyoplankton surveys must be combined with complementary information from IA and PAT tagging efforts on adults. Using surface-flow models that

integrate eddy formation and movement, studies should be conducted to retrospectively determine the hatching/spawning locations. Efforts to delineate spawning grounds using hydrodynamic models and archival tags are already underway by researchers from the TAG Program and such information will be needed to develop prudent strategies for limited time-area closures.

3. Expand investigations of movement and stock structure and determine the contribution levels of individuals of each stock on mixing grounds of the western Atlantic and the central North Atlantic. While we have made progress on the issues of stock structure and mixing using archival tags, otolith chemistry, and molecular genetics, these tools can now be applied on either much larger samples (otolith chemistry and molecular genetics) or targeted/representative samples (archival tags) to address key hypotheses related to the contribution rates of source populations to mixed stock fisheries, reproductive schedules and behavior, and the classification of seasonal and ontogenetic migration pathways for each stock. An improved understanding of age-specific migration within each stock (contingent structure) will contribute significantly to spatial management regimes, and this may be best accomplished by combining approaches (e.g., obtaining archival tag, otolith chemistry, and genetic data from the same individual).
4. Characterize natal homing behavior to spawning grounds in the Gulf of Mexico and Mediterranean Sea. Although data from electronic tags suggests that individuals return to natal sites and do not visit more than one spawning area in their lifetime, archival tag releases should be increased in both the eastern and western Atlantic to provide more information on spawning migrations and behavior. Moreover, characterization of natal origin of *T. thynnus* on spawning grounds in the Gulf of Mexico and Mediterranean Sea should be determined using natural markers (e.g., stable isotopes in otoliths).
5. Develop a valid age determination procedure. Bomb radiocarbon dating represents one of the most robust methods for validating age determination methods for *T. thynnus*. Other methods could include radiometric dating and pen-rearing experiments, similar to investigations on *T. maccoyii* conducted over a decade ago. Age determination is the cornerstone of accurate assessments and biological reference points, directing priority on development of an accurate and precise procedure.

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