CHAPTER 2.1.5:	**AUTHOR:**	**LAST UPDATE:**
ATLANTIC BLUEFIN TUNA	**J-M. FROMENTIN**	**Nov. 14, 2006**

2.1.5 Description of Atlantic Bluefin Tuna (BFT)

1. Names

1.a Classification and taxonomy

Species name: *Thunnus thynnus* (Linnaeus 1758)
ICCAT species code: BFT
ICCAT names: Atlantic Bluefin tuna (English), Thon rouge de l'Atlantique (French), Atún rojo del Atlántico (Spanish)

According to Collette *et al.* (2001), bluefin tuna is classified as follows:

- Phylum: Chordata
- Subphylum: Vertebrata
- Superclass: Gnathostomata
- Class: Osteichthyes
- Subclass: Actinopterygii
- Order: Perciformes
- Suborder: Scombroidei
- Family: Scombridae
- Tribe: Thunnini

1.b Common names

List of vernacular names used according to ICCAT and Fishbase (www.fishbase.org). The list is not exhaustive and some local names might not be included.

Albania: Toni
Angola: Atum, Rabilha
Argentina: Atún aleta azul, Atún rojo
Brazil: Albacora-azul, Atum, Atum-azul, Atum verdadeiro, Rabilo
Bulgaria: Ton
Canada: Bluefin tuna, Thon rouge, Squid hound
Cape Verde: Atuarro, Atum-azul, Atum-de-direito, Atum-de-revés, Atum-rabil, Atum-rabilho, Rabão
Chile: Atún cimarrón, Atún de aleta azul
China: Cá chan, Thu
Chinese Tapei: Hay we
Colombia: Atún, Atún de aleta azul
Croatia: Tuna plava, Tunj
Cuba: Atún aleta azul
Denmark: Almindelig Tun, Atlantisk tun, Blåfinnet tun(fisk), Tun(fisk)
Dominican Rep.: Atun
Egypt: Tunna
Faeroe Is: Tunfiskur
Finland: Tonnikala
France: Thon rouge, Ton France, Auhopu
Germany: Atlantischer Thunfisch, Roter Thun, Thunfisch
Greece: Τόνος, Όρκυνος, Κόπανος, Ορτσίνι, Μαγιάτικο, Γλουπέας, Γοφός, Tónnos, Tonos
Iceland: Túnfiskur
Ireland: An tuinnín, Bluefin tuna

Israel: Tunna kehula
Italy: Tonno, Ton, Tonne, Tunnu, Tunina, Tunnachiula, Barilaro, Franzillottu
Japan: Kuromaguro
Korea: Cham-da-raeng-i
Lebanon: T'oûn ah'mar
Malta: Tonn, Tonnu, Tunnagg
Marshall Is: Boebo
Mexico: Atún aleta azul
Morocco: Thone
Netherlands: Tonijn
Norway: Thunfisk, Makrellshørje, Sjorje
Oman: Tunna
Peru: Atún de aleta azul
Poland: Ton, Tunczyk blekitnopletwy
Portugal: Atum, Atum rabil, Atum-rabilho, Mochama
Romania: Ton, Ton rosu
Russia: Siniy, Krasnyj/Sineperyj/Sinij/Solsheglazyj/Zoludoj/Vostochnyj tunets
Senegal: Waxandor
SerbiaMontenegro: tuna
South Africa: Bluefin tuna, Blouvin-tuna
Spain: Atún, Atún rojo, Golfàs, Tonyina
Sweden: Tonfisk, Röd tonfisk, Makrillstörje
Tunisia: Toun ahmar
Turkey: Orkinos, Orkinoz baligi, Ton baligi
Ukraine: Obyknovennyi tunets
United-Kingdom: Northern bluefin tuna, Bluefin tunny
Uruguay: Atún rojo, Aleta azul
United States: Bluefin tuna

2. Identification

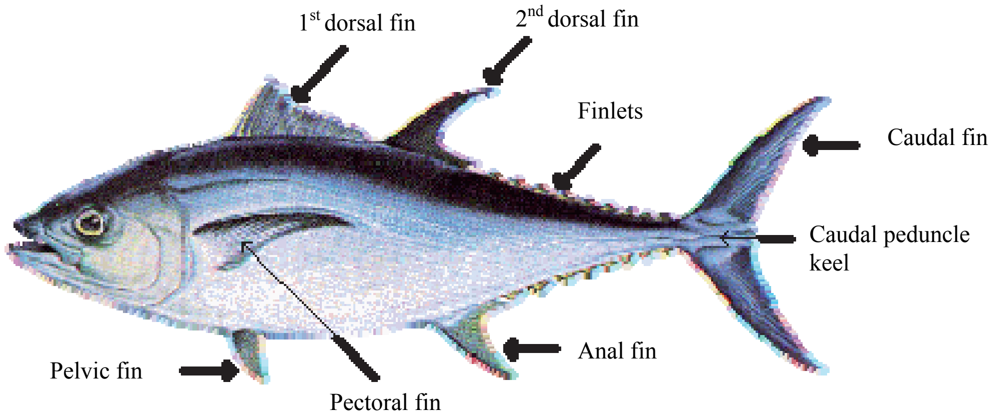


Figure 1. Drawing of an Atlantic bluefin tuna. Source: Fisheries Global Information System from FAO (http://www.fao.org/figis/servlet/static?dom=root&xml=speciesgroup/data/tunalike.xml).

Atlantic bluefin tuna (BFT) is the largest tuna species. It has an elongated fusiform body, being more robust at the front. Its maximum length can exceed 4 m long. Its official maximum weight is 726 kg, but weights up to 900 kg have been reported in various fisheries of the West Atlantic and Mediterranean Sea (Mather *et al.* 1995).

BFT body is deepest near the middle of the first dorsal fin base. The back is dark blue, while lower sides and belly are silvery white with colorless transverse lines alternated with rows of colorless dots. Bluefin tuna displays 39 vertebrae and 12 to 14 dorsal spines and 13 to 15 dorsal soft rays. The first dorsal fin is yellow or bluish; the second dorsal fin, which is higher than the first, is reddish-brown. The anal fin and finlets are dusky yellow and edged with black; the median caudal keel is black in adults. Swim bladders are present and the pectoral fins are very short, less than 80% of head length.

3. Biology and population studies

3.a Habitat

Atlantic bluefin tuna inhabit the pelagic ecosystem of the entire North Atlantic and its adjacent seas, primarily the Mediterranean Sea **(Figure 2)**. Among the tuna, bluefin tuna has the widest geographical distribution and is the only large pelagic fish living permanently in temperate Atlantic waters (Bard *et al.* 1998; Fromentin and Fonteneau 2001). Archival tagging and tracking information confirmed that bluefin tuna can sustain cold (down to 3°C) as well as warm (up to 30°C) temperatures, while maintaining stable internal body temperature (e.g. Block *et al.* 2001).

Until recently, it was hypothesised that bluefin tuna mostly occupies the surface and subsurface waters of the coastal and open-sea areas, but archival tagging and ultrasonic telemetry have revealed that both juveniles and adults bluefin tuna frequently dive to depth of 500m to 1000m (e.g. Brill *et al.* 2001; Lutcavage *et al.* 2000).

Similar behaviour has also been reported for southern bluefin tuna, bigeye tuna and swordfish and is generally associated to foraging in deep scattering layers and/or to physiological constraints to cool the body temperature (Gunn and Block 2001; Musyl *et al.* 2003). For this reason, bluefin tuna habitat, as this of other tuna and billfish, needs to be described in three dimensions (Brill and Lutcavage 2001).

The spatial distribution and movement of bluefin tuna have been traditionally hypothesized to be controlled by preferential ranges and gradients of temperature, similar to other tuna species (Inagake *et al.* 2001; Laurs *et al.* 1984; Lehodey *et al.* 1997).

Recent works appear to converge toward the opinion that juvenile and adult bluefin tuna frequent and aggregate along ocean fronts (Humston *et al.* 2000; Royer *et al.* 2004). This association is also likely to be related to foraging, bluefin tuna feeding on the abundant vertebrate and invertebrate prey concentrations of these areas.

The types of ocean fronts known to be frequently visited by bluefin tuna are upwelling areas, such the West coasts of Morocco and Portugal, and meso-scale oceanographic structures associated with the general circulation of the North Atlantic and adjacent seas (Bard *et al.* 1998; Boustany *et al.* 2001; Farrugio 1981; Mather *et al.* 1995; Wilson *et al.* 2005). Despite this general agreement, bluefin tuna habitat appears more complex than what could be explained by these oceanic features, alone, and much more remains to be learned (Royer *et al.* 2004; Schick *et al.* 2004).

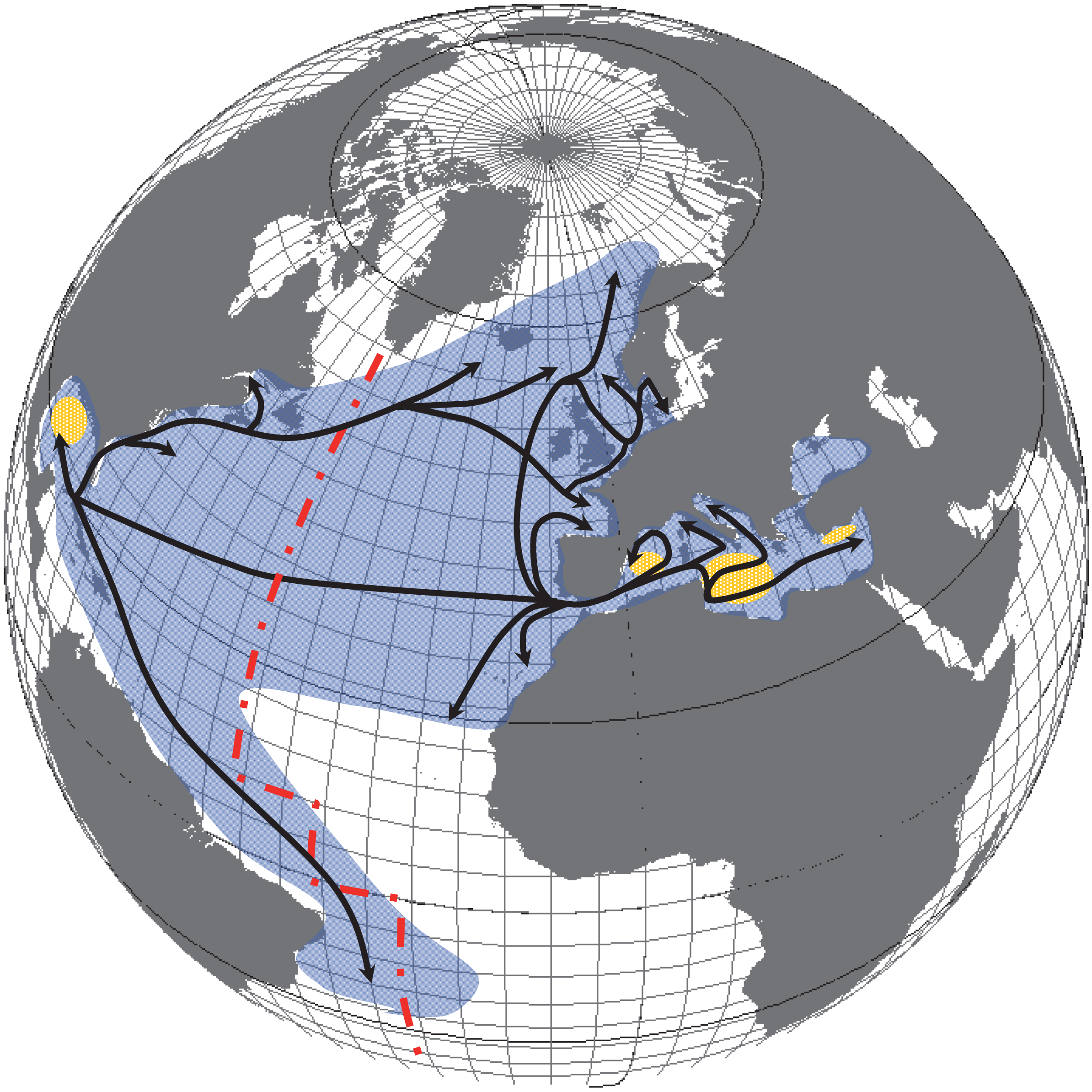


Figure 2. Map of the spatial distribution of Atlantic bluefin tuna (blue), main migration routes (black arrows) and main spawning grounds (yellow areas) deduced from current and historical fisheries data as well as traditional and electronic tagging information. The vertical dashed line depicts the stock delimitation between the two current ICCAT management units (modified after Fromentin & Powers 2005).

3.b Migration

Bluefin tuna migration in the Mediterranean Sea have been described long ago by the ancient Greek and Latin philosophers, especially Aristotle (IV B.C.) and Pliny the Elder (Ith A.C.). A migratory connection between oceans was first mentioned by Cetti (1777), who suggested that bluefin tuna come into the Mediterranean from the North Atlantic to spawn around Sicily and then go back by the same routes.

This hypothesis has been later argued by Pavesi (1889), who postulated, on the basis on observations from the trap fisheries, that the Mediterranean Sea displays a separate BFT stock from this of the North Atlantic. This hypothesis, known as the ‘native hypothesis’, remained dominant for several decades and was accepted by several authors, e.g. de Buen (1925), Roule (1917).

It was finally questioned when some hooks used in the North Atlantic were found on fish caught in the Mediterranean (Heldt 1929; Sella 1929). Migration between the Mediterranean and North Atlantic was definitively accepted during the 1960s and 1970s based on a large set of the recaptures of conventional tags and has been re-confirmed by many observations since then (e.g. Mather *et al.* 1995, **Figures 2 and 3**).

These migration patterns have led to the hypothesis of a homing behaviour, i.e. bluefin tuna migrate to spawn in specific and well defined areas (Cury 1994; Fromentin and Powers 2005). An hypothesis that is supported by recent electronic tagging experiment, which show spawning site fidelity in both the Mediterranean Sea and Gulf of Mexico (Block *et al.* 2005).

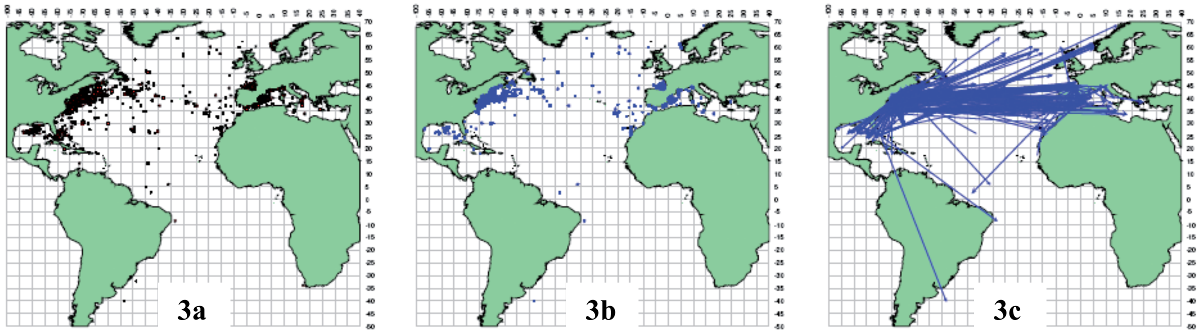


Figure 3. Summary of conventional tag releases and recoveries from the ICCAT database (Source: ICCAT Statistical Bulletin, Vol. 35). 3a: distribution of releases, 3b: distribution of recoveries and 3c: direct trajectories between releases and recoveries.

Little is known about feeding migrations within the Mediterranean and the North Atlantic, but results from electronic tagging indicated that migration and movement patterns of bluefin tuna vary considerably between individuals, years and areas (Block *et al.* 2001; de Metrio *et al.* 2002; Lutcavage *et al.* 1999).

The appearance and disappearance of past fisheries also suggest that important changes in the spatial dynamics of bluefin tuna may be environmentally driven (Marsac 1999; Ravier and Fromentin 2004). After examining size composition of the bluefin tuna catches of the Norwegian and German fisheries, Tiews (1978) postulated that the sudden collapse of these fisheries in 1963 resulted from a lack of migrating mature tunas in the northern area. Similarly, the sudden appearance/disappearance of bluefin tuna offshore the Brazilian coasts during the 1960s is likely to result from changes in bluefin tuna spatial distribution and/or migration (Fromentin and Powers 2005).

3.c Population structure

Understanding bluefin tuna migratory behaviour is crucial for management, as spatial variability governs the definition of management units, stocks and boundaries. ICCAT currently manages BFT as two stocks with the boundary between the two spatial units being the 45°W meridian (**Figure 2**). This delimitation was originally established for management convenience (see ICCAT 2002a), but it has been recently criticised, as higher rates of trans-Atlantic migration than previously suspected have been detected through electronic tagging.

For instance, if Block *et al.* (2005) still advocated for distinct spawning areas between East and West Atlantic stocks, these authors also postulated that significant overlapping distribution on North Atlantic feeding grounds; an hypothesis already raised by several past authors, such as Tiews (1963) or Mater *et al.* (1995).

Electronic tagging has considerably improved our understanding of bluefin tuna spatial dynamics, but it does not provide the location of birth of the migrating fish; a key information to understand the population structure. Chemical signatures in hard structures (especially otolith) have shown to be helpful to discriminate between putative nursery grounds of West Atlantic and Mediterranean bluefin tuna (Rooker and Secor 2004; Rooker *et al.* 2003; Rooker *et al.* 2002).

The hypothesis of genetic stock structure in bluefin tuna populations has also been investigated using various genetic markers (e.g. Carlsson *et al.* 2004; e.g. Ely *et al.* 2002; Pujolar and Pla 2000; Viñas *et al.* 2003). Although the results remain somewhat controversial, most recent and extensive studies (Carlsson *et al.* 2004; 2006) tend to support the hypothesis of a complex population structure, with, for instance, genetic differences within the Mediterranean Sea and the central North Atlantic.

These results, together lesson from bluefin tuna fisheries history, lead Fromentin and Powers (2005) to postulate that Atlantic bluefin tuna may be seen as a metapopulation, i.e. a collection of discrete local populations, occupying distinct and patchy suitable habitats and displaying their own dynamics (including migration), but with a degree of demographic influence from other local populations through dispersal. Such a hypothesis might provide a better framework to explain the concomitance of homing behaviour with the occurrence of colonization and extinction in some areas (i.e. Brazil and North Sea).

4. Biology

4.a Maturity

Various past studies showed that Atlantic bluefin tuna mature at 110-120cm (25-30kg) in the East Atlantic and Mediterranean Sea, so at approximately 4 years old (according to the East and Mediterranean growth curve, see **Table 1 and Figure 4**). The size of the fish spawning in the Gulf of Mexico were always greater than 190cm, which would correspond to about 8 years old (according to the western growth curve, **Table 1 and Figure 4**). This disparity in age-at-maturity between West Atlantic and Mediterranean bluefin tuna has been used as a major argument for separation into two stocks. Related species, such as the Pacific bluefin tuna (*Thunnus orientalis*) and southern bluefin tuna (*Thunnus maccoyii*), appear to mature as late as West Atlantic bluefin tuna (from 8 to 12 years depending on the authors, (Caton 1991; Schaefer 2001).

Table 1. Age, size and weight at maturity for the East Atlantic & Mediterranean bluefin tuna and the West Atlantic bluefin tuna.

	East Atlantic & Mediterranean Sea	***West Atlantic***	***References***
First age and size-at-maturity	Age 3 100cm / 20kg	Age 5 140cm / 45kg	Mather *et al.* 1995
50% maturity	Age 4 115cm / 30kg	Age 8 190cm / 120kg	Mather *et al.* 1995 ICCAT 1997
100% maturity	Age 5 135cm / 50kg	Age 10+ 220cm / 175kg	Mather *et al.* 1995 Diaz & Turner 2007

Recent progress has been made in the determination of maturity by measuring hormone concentrations in blood (Susca *et al.* 2001). These new techniques have confirmed the early length-at-maturity (at around 120 cm) for BFT female in the Mediterranean Sea (ICCAT 2003b). Most recent studies in the West Atlantic tend to advocate for an even later age-at-maturity, i.e. 10 to 12 years (Diaz and Turner 2007).

After several decades of studies, age-at-maturity remains uncertain for the Atlantic bluefin tuna, especially for the West Atlantic (depending on the authors, the 50% maturity varies between age 5 and age 12). Further investigations are thus still needed, using for instance the same sampling protocol and same methodology on both sides of the Atlantic (Fromentin and Powers 2005).

4.b Sex-ratio

The proportion of males appears to be higher in catch samples of large individuals, which could be due to a higher natural mortality or lower growth for females (ICCAT 1997). A recent study done by de la Serna *et al.* (2003) indicated that such differences may vary among gears and areas (e.g. between Gibraltar straits and Western Mediterranean), but in all cases the authors found about 80% of males among fish greater than 250cm. In contrast, Hattour (2003) has found higher or equal (depending on the year) proportion of females for all size-classes in the catches of purse seiners operating in the central Mediterranean.

4.c Spawning and reproduction

Bluefin tuna is oviparous and iteroparous, as all tuna species (Schaefer 2001). It has asynchronous oocyte development and is a multiple batch spawner (spawning frequency being estimated at 1-2 days in the Mediterranean, Medina *et al.* 2002). Egg production is age (or size)-dependent: a 5-years old female produces an average of five million eggs (of ~1mm), while a 15-20 years female can carry up to 45 million eggs (Rodriguez-Roda 1967).

Average fecundity was recently estimated from stereological quantification at around 93 oocytes/g of body mass for the East Atlantic bluefin tuna (Farley and Davis 1998; Medina *et al.* 2002; which is comparable to that found for other tuna Schaefer 2001). It is generally assumed that bluefin tuna spawns every year, but electronic tagging experiments, as experiments in captivity, suggest that individual spawning might occur only once every two or three years (Lutcavage *et al.* 1999).

It is generally agreed that BFT spawning takes place in warm waters (> 24°C) of specific and restricted locations (around the Balearic islands, Sicily, Malta, Cyprus and some areas of the Gulf of Mexico, Figure 2) and occurs only once a year in May-June (Karakulak *et al.* 2004; Mather *et al.* 1995; Nishikawa *et al.* 1985; Schaefer 2001). In contrast with tropical tuna, BFT reproduce within a small spatial and temporal window (Fromentin and Fonteneau 2001). However, other spawning grounds, such as the Ibero-Morrocan embayment and the Black Sea, have also been mentioned in the past (e.g. Picinetti and Piccinetti Manfrin 1993).

Bluefin tuna spawns when they reached specific locations (Mather *et al.* 1995; Rodriguez-Roda 1964). Medina et al. (2002) showed that the time that separates the occurrence of the migrating fish in the Strait of Gibraltar and the spawning in the Balearic area, is short and does not exceed a few weeks. This rapid gonadal development is possibly related to increasing water temperature. Spawning fertilization occurs directly in the water column and hatching happens without parental care after an incubation period of 2 days.

4.d Recruitment

Fish larvae (around 3-4 mm) are typically pelagic with a yolk sac and relatively undeveloped body form. The yolk sac is desorbed within few days. Little is known about the effects of the age-structure of the spawning stock, as well as the condition of the spawners, on the viability of the offspring, but recent studies on groundfish or rockfish have demonstrated that such relationship may be crucial for long-live fish species (Berkeley *et al.* 2004; Birkeland and Dayton 2005; Cardinale and Arrhenius 2000; Marteinsdottir and Begg 2002).

It was suggested that the North Atlantic Oscillation (NAO) might affect bluefin tuna recruitment success in the East Atlantic, but further statistical analyses did not confirm such hypothesis (ICCAT 2002b). The identification of the major abiotic and biotic forces controlling bluefin tuna recruitment remains thus obscure. The degree of complexity of population structure on the one hand (Fromentin and Powers 2005) and the potential impact of environmental changes on the migratory behaviour (Ravier and Fromentin 2004) could strongly affect the reproductive strategy and recruitment success of bluefin tuna.

4.e Diet

Like many marine fish, bluefin tuna larvae appear to feed primarily on small zooplankton, mainly copepods and copepoda nauplii (Uotani *et al.* 1990). As are most predators, juvenile and adult bluefin tuna are opportunistic feeders. Chase (2002) enumerated more than 20 species of fish and about 10 of invertebrates in the bluefin tuna stomach. The diet can also include jellyfish and salps, as well as demersal and sessile species such as, octopus, crabs and sponges. In general, juveniles feed more on crustaceans, fish and cephalopods, while adults primarily feed on fish, mostly herring, anchovy, sand lance, sardine, sprat, bluefish and mackerel (Eggleston and Bochenek 1990; Ortiz de Zarate and Cort 1986).

Bluefin tuna stomach contents are, however, dominated by one or two prey-species, such as Atlantic herring and sand lance in the West Atlantic or anchovy in the East Atlantic and Mediterranean. No clear relationship has been demonstrated between prey length and the size of bluefin tuna; both small and large bluefin tuna display similar prey-size spectra. However, Chase (2002) noted that the largest prey (those greater than 40cm) were only consumed by giant bluefin tuna > 230cm.

4.f Growth

The ageing procedure for bluefin tuna has mostly been based on the count of marks on hard structures, but a few studies were also based on length-frequency and mark-recapture data. Still, age-size relationships remain uncertain, especially for older individuals (> 8 years).

The count of annuli on otoliths, spines, vertebrae and scales are indeed impaired by various sources of errors, such as the coalescence or the disappearance of the first marks or conversely to the multiple marking due to migration patterns (see Compean-Jimenez and Bard 1980; Compean-Jimenez and Bard 1983; Cort 1991; Farrugio 1981; Mather *et al.* 1995).

Decomposition of bluefin tuna length-frequency data into age-classes becomes difficult for fish older than 5 years, as the cohorts tend to become indistinguishable (Fromentin 2003).

Mark-recapture based growth curves used for ageing do neither perform well for fish greater than 200 cm (~10 years old). This is due to the scarcity of observations and high variability in growth for these sizes (Turner *et al.* 1991).

Consequently, there is considerable variation between the von Bertalanffy equations estimated by various authors (**Table 2**). The age estimate for a fish of 1m and 2 m in length ranges over 3 and 6 years, respectively.

Table 2. Parameters of Von Bertalanffy equations as estimated for various area and technique or methodology by various authors (this list is not exhaustive and include studies based on large sample sizes).

Sources	***Area***	***Methodology***	***L∞***	***k***	***to***
Sella (1929)	Mediterranean	Vertebrae	499.68	0.044	-2.114
Westmann & Gilbert (1941)	West Atlantic	Scales	197.94	0.196	-0.778
Mather & Schuck (1960)	West Atlantic	Vertebrae	437.46	0.055	-1.489
Rodriguez Roda (1964,1969)	East Atlantic	Vertebrae	355.84	0.090	-0.890
Caddy *et al.* (1976) males	West Atlantic	Otolith	286.64	0.134	0.328
Caddy *et al.* (1976) femelles	West Atlantic	Otolith	277.31	0.116	0.800
Farrugio (1981)	Mediterranean	Vertebrae	351.13	0.080	-1.087
Cort (1991)	East Atlantic	Spines	318.85	0.093	-0.970
Turner and Restrepo (1994)	West Atlantic	Mark-recapture	382.00	0.079	-0.707

The application of more advanced technologies such as electronic microscopes used to investigate the annuli on hard structures or electronic tagging to get precise spatial and temporal information may help in distinguishing between observation error and process error. Innovative modelling approaches, such as the growth model developed by Evenson *et al.* (2004), which integrates data from the three key sources (length-frequency, tag-recapture and hard structures) within the same estimation framework could and should be applied to bluefin tuna. Juvenile growth is rapid for a teleost fish (about 30cm/year), but somewhat slower than other tuna and billfish species (Fromentin and Fonteneau 2001). Fish born in June are about 30-40cm long and weigh about 1 kg by October. After one year, fish reach about 4 kg and 60cm long (Mather *et al.* 1995).

Growth in length tends to be lower for adults than juveniles, but growth in weight increases (**Figure 4**). Therefore, juveniles are relatively slim, whereas adults are thicker and larger. In average, an individual bluefin tuna is about 200cm and 150kg at 10 years old and reaches about 300cm and 400kg at 20 years.

Fish of 685kg has been reported in Italian trap catches and an individual of 427cm and 726kg has been caught in the Gulf of Maine (Bigelow and Schroeder 1953; Sara 1969).

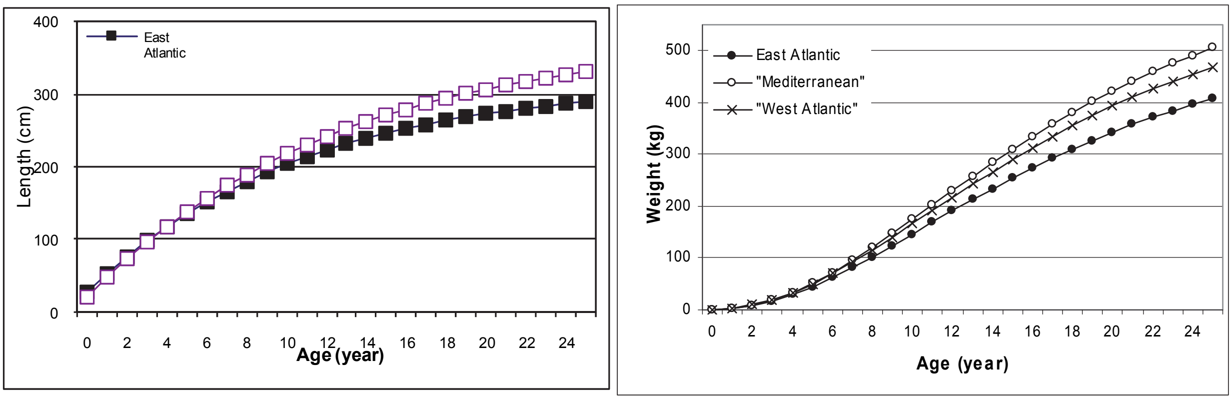


Figure 4. Length (left panel) and weight (right panel) curves for the East Atlantic, Mediterranean and West Atlantic (see **Tables 1 and 2**).

A few studies also suggest that males grow faster than females and are proportionally more frequent in catches of individuals larger than 250cm (see above). Some differences have been noted between West Atlantic, East Atlantic and Mediterranean Sea (**Figure 4**), but some disparities also appear among the various Length-Weight relationships that have been reported within each area. The current ICCAT L-W equations for the East Atlantic and Mediterranean are poorly documented (**Table 3**).

Table 3. ICCAT Length-weight relationship for the East Atlantic, Mediterranean and West Atlantic bluefin tuna.

Sources	*Area*	*Equation*
ICCAT 1984	East Atlantic	$W=2.95.10^{-5}*FL^{2.899}$
ICCAT 1984	Mediterranean	$W=1.96.10^{-5}*FL^{3.009}$
Parrack and Phares (1979)	West Atlantic	$W=2.861.10^{-5}*FL^{2.929}$

Seasonal growth patterns have been better documented. Both juvenile and adult grow rapidly during summer and early autumn (up to 10% per month), while growth is negligible in winter (Labelle *et al.* 1997; Mather *et al.* 1995; Tiews 1957). Additionally, significant year-to-year and decadal variations in weight-at-age of juveniles in the Western Mediterranean Sea have been also depicted (Fromentin 2003).

4.g Natural mortality

Like many fish populations, natural mortality rates (M) are poorly known for bluefin tuna. However, it is generally agreed that: (i) long-lived fish, such as bluefin tuna, have a lower and less variable M than short-lived ones, (ii) M's are higher during juvenile stages than during the onset of adulthood (disregarding senescence), and (iii) M's also vary with population density, size, sex, predation and environment (e.g. Vetter 1987).

As bluefin tuna is a highly migratory and pelagic species, competition and cannibalism due to food and/or habitat limitations are expected to be lower than for groundfish. Predation purportedly comes mainly from large pelagic sharks and killer whales, as depicted at the entrance of the Gibraltar Straits during bluefin tuna spawning migration (Nortarbartolo di Sciara 1987). Tagging from Southern bluefin tuna (*Thunnus maccoyii*) tends to confirm that M is higher for juveniles (between 0.49 and 0.24) compared to that of adults (around 0.1).

In the absence of direct and consistent estimates of M for Atlantic bluefin tuna, the natural mortality vector of the Southern bluefin tuna is generally used for the East-Atlantic and Mediterranean stock assessment, whereas a constant M of 0.14 is assumed for the West Atlantic bluefin tuna (ICCAT 1999; ICCAT 2003a). However, both solutions remain unsatisfactory and tagging experiments and modelling are needed to progress on this issue.

4.h Life history traits

Table 4. Life history traits of the 10 selected tunas and tuna-like species as collected from the literature from Fromentin and Fonteneau 2001).

Species	*Spawning duration (month/yr)*	*Length at mat. (cm)*	*Weight at mat. (kg)*	*Age at mat. (year)*	*Max. length (cm)*	*Max. weight (kg)*	*Max. age (year)*	*Juvenile growth* $(\%L.yr^{-1})$
Skipjack	12	45	1.7	1.5	75	23	4.5	40
Atlantic little tuna	12	42	-	1.5	85	12	6	32.9
Yellowfin tuna	6	105	25	2.8	170	176	7.5	22.1
Bigeye tuna	3	115	31	3.5	180	225	6	18.3
Atlantic sailfish	2	130	16	3	255	-	18	17
Atlantic white marlin	4	130	20	3	260	-	15	16.7
Albacore (North Atlantic)	3	90	15	4.5	120	80	9.5	16.7
Swordfish (North Atlantic)	3	175	70	5	290	650	17	12.1
Bluefin tuna (East Atlantic)	1.5	115	27.5	4.5	295	685	20	8.7
Southern bluefin tuna	2	130	43	8	200	320	19	8.1

There is thus a clear contrast between bluefin tuna life history traits and these of other tuna species, especially tropical tuna (**Table 4**).The latter are indeed characterized by a rapid growth, an early age-at-maturity, continuous spawning, a limited maximum size, a short life span and a distribution restricted to warm waters, whereas bluefin tuna typically displays opposite characteristics similar to cold-water species, i.e. slower growth, later maturity, shorter spawning season, larger size and longer life span (Fromentin and Fonteneau 2001). These life history traits make thus bluefin tuna more vulnerable to exploitation than tropical tuna, as its population growth rate is lower.

5. Fisheries

5.a Ancient Fisheries History

Archaeological excavations have shown that fishing on bluefin tuna has occurred in the Mediterranean since the 7th millennium BC (Desse and Desse-Berset 1994). About a hundred separate fisheries targeting tuna, bonito and sardine were established (along with salting plants) by the Phoenicians, then by the Romans around the Western Mediterranean Sea (Doumenge 1998; Farrugio 1981; Mather *et al.* 1995). At that time, fishermen primarily used hand lines and several varieties of seines, particularly beach seines.

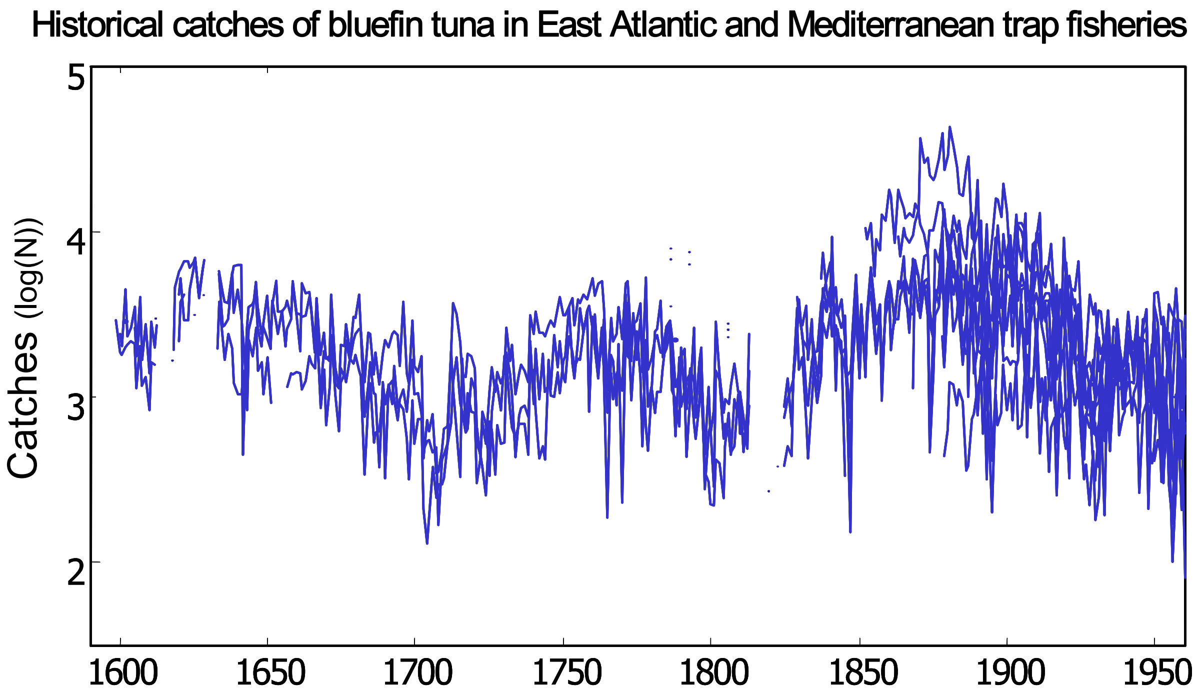


Figure 5. Long time series (between 80 and 360 years long) of bluefin tuna catches from 8 traps set along Portugal, Sardinia, Sicily and Tunisia between 1599 and 1960 (catches are expressed in the log-number of fish caught over a given year.

Bluefin tuna exploitation remains active in the Middle-Age and beach seines were progressively replaced by traps since the 16th century (Doumenge 1998; Ravier and Fromentin 2001). Traps and beach seines were used throughout the Mediterranean and Gibraltar strait and were the first industrial fisheries in this area. These fisheries comprised an important use of labour for fishing and canning and substantial capital investment (Berthelot 1988; Doumenge 2000; Pavesi 1889).

Historical information from national and private archives, scientific libraries and various Mediterranean laboratories have been collated, and then analysed, through the European scientific program STROMBOLI. It appears that the trap yields fluctuated between 7,000 and 30,000 tonnes per year, with a mean range of about 15,000 tonnes per year (Ravier and Fromentin 2002). These estimates confirmed the intensity of bluefin tuna exploitation by the ancient trap fisheries cited previously by historians.

The trap catches further display a dominant 100-120 years periodic fluctuation **(Figure 5,** see also Ravier and Fromentin 2001**)**. Since these long-term fluctuations were synchronous between areas of the Western Mediterranean and near North Atlantic (over a distance of some to 2,500 km), it was postulated that this pseudo-cycle reflected variations in bluefin tuna abundance of entering the Mediterranean each year for spawning.

In a subsequent analysis, Ravier and Fromentin (2004) showed that these long-term variations in trap catches were inversely related to temperature and could, therefore, result from changes in migration patterns of bluefin tuna spawners in response to modifications in oceanographic conditions.

5.b Recent fisheries history

Traps underwent few technical modifications until the early 20th century, but increasing coastal traffic, noise, and coastal pollution may have contributed to a reduction of the trap efficiency at the beginning of the 20th century (Addis *et al.* 1997; Ravier and Fromentin 2001). Until that period, bluefin tuna fishing primarily occurred in the Mediterranean Sea and the Ibero-Moroccan embayment, but exploitation progressively expanded during the 19th century.

A hand line fishery targeting juveniles bluefin tuna and North Atlantic albacore arose in the Bay of Biscay during the mid-19th century (which is still in activity, but nowadays mainly composed by bait boats, Bard 1981). bluefin tuna was also occasionally caught in the North Sea, Norwegian Sea and Kattegat since the 1930s by hook and line and, later, by purse seine (Meyer-Waarden 1959).

These Nordic fleets grew rapidly such that their yields exceeded that of the traditional trap fisheries during the 1950s (up to 16,000 t/year, **Figures 6 and 7**). Their catches were mainly composed of large bluefin tuna migrating North in summer to feed on pelagic fish, such as herring and sprat (Hamre *et al.* 1968; Pusineri *et al.* 2002). The Norwegian fleet, which caught about 80% of the total Nordic catch, was the only one remaining active after the sudden collapse in 1963, possibly due to changes in migration patterns (Tiews 1978).

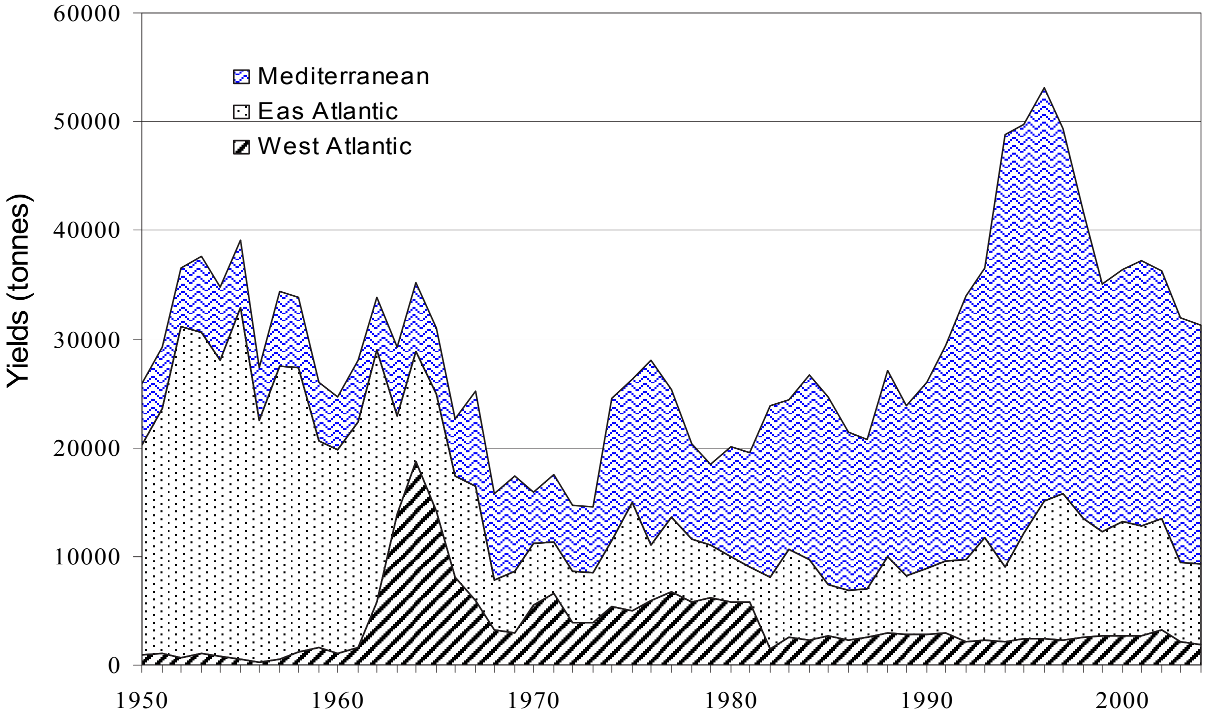
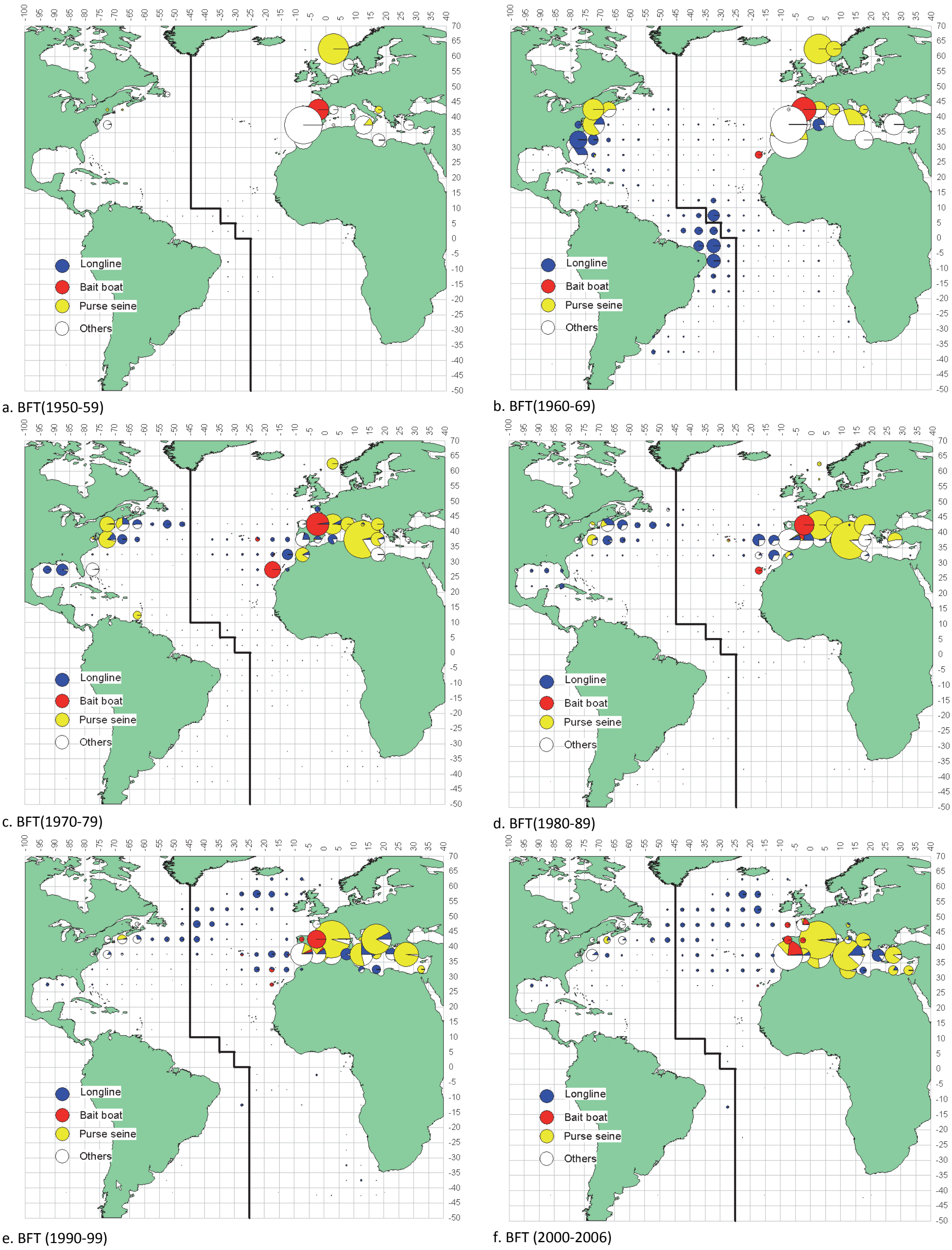


Figure 6. Reported Catches (in t) to ICCAT Secretariat of bluefin tuna by main area (Source, ICCAT 2007).

During the 1960s, fisheries also emerged along the edge of the western Atlantic continental shelf, especially between Cape Hatteras and Newfoundland (Mather *et al.* 1995). Fisheries for juveniles were conducted by purse seines extending northward to Cape Cod and Maine in the 1950s and 1960s (**Figure 7**).

Additionally, small fisheries for large fish were conducted by handlines, traps, harpoons and rod and reel. However, markets for large fish were not fully developed and demand for these fish was low. Longlining in oceanic waters of the western Atlantic also developed in the 1960s, primarily by Japan. The longliners focused primarily on medium-sized fish, but concentrations of large fish were exploited if encountered, e.g. offshore the Brazilian coast between 1962 and 1967. During the 1970s, these fisheries moved to the Gulf of Mexico to target large fish.

The late 1960s and early 1970s were a transitory period for both the Atlantic and Mediterranean BFT fisheries. The landings were lower than in the previous decades (about 12,000 t/year, **Figure 6**), because of the decreasing activity of the traps and Nordic fleets in the East Atlantic and a reduction in purse seine catches of juveniles in the West Atlantic. Also during that period, purse seine and long-line fleets progressively replaced the traditional fisheries of the Mediterranean and East Atlantic (**Figure 7**).



a. BFT(1950-59)

b. BFT(1960-69)

c. BFT(1970-79)

d. BFT(1980-89)

e. BFT (1990-99)

f. BFT (2000-2006)

Figure 7. Total catches of BFT per decade, 5°x5° squares and main gear (Source: ICCAT Statistical Bulletin Vol. 37).

The development of the Japanese sushi-sashimi market during the 1980s was the most remarkable event of the recent decades, as it made bluefin tuna exploitation much more profitable than before (Fromentin and Ravier 2005; Porch 2005). Consequently, there was a sharp increase in the efficiency and capacity of the established fisheries during the 1980s and 1990s, especially in purse seiners.

Furthermore, novel storage technologies (such as carrier vessels with deep freezing storage) and, more recently caging systems (for holding and fattening fish) were recently introduced and greatly modified both fishing strategies and efficiency. These profitable conditions (the value of a fish put into cage is about double that of a frozen fish of high quality) also induced a rapid development of new and powerful fleets, especially in the Mediterranean countries.

Consequently, the fishing areas economically available for exploitation expanded in both the North Atlantic and Mediterranean (**Figure 7**). The Mediterranean Sea is a typical example of this. While traditional ABFT fisheries mostly operated along specific areas of the coasts until the mid-1980s (e.g., the Gulf of Lions, the Ligurian, Ionian and Adriatic Seas), the fisheries rapidly expanded over the whole Western basin during the late 1980s and early 1990s and more recently over the Central and Eastern basins, so that bluefin tuna is now exploited over the whole Mediterranean Sea for the first time in its long millennial fisheries history.

The expansion of the Japanese long line fleets in the Central North Atlantic mostly along the Gulf Stream during the 1990s was also a new feature (**Figure 7**). The redistribution of all the fisheries resulted in rapid increases in yields since the 1980s, especially in the Mediterranean Sea (**Figure 6**). Catches in the East Atlantic and Mediterranean reached an historical peak exceeding 50,000 tonnes during the mid 1990s.

Subsequent reductions in the magnitude of landings are questionable, since under-reporting may have occurred after the implementation of a TAC (Fromentin 2003; ICCAT 2005). Last estimates from the SCRS indicated that catches over the last decade have probably remained at around 50,000 tonnes for the East Atlantic and Mediterranean Sea (ICCAT 2007). Catches of the West Atlantic have not varied very much since 1982 due to the imposition of management quotas (the range over this period is 2,100 to 3,000 tonnes, **Figure 6**).

The spatial expansion of many fisheries, together with new outcomes from electronic tagging, that demonstrated more substantial movement of large Atlantic bluefin tuna from West to East Atlantic/Meditarrenean than previously thought, have questioned again the validity of the 45°W meridian as an appropriate management boundary *(e.g.* Block *et al.* 2001; Lutcavage *et al.* 2001). Alternative assessment methods which incorporate movement, in particular movement and mixing models focused on diffusion or overlap, have been developed (Porch *et al.* 2001; Powers and Cramer 1996) and operating models, i.e. models integrating biological realism with robust management procedures, are currently investigated to tackle this issue (e.g. Kell *et al.* 2003; Powers and Porch 2004).

5.c Main management regulations

In 1981, the Commission set a “scientific monitoring level” for the West Atlantic stock, i.e. a TAC that was negotiated within the Commission. The goal was to set the level low enough to initiate recovery. In 1998, ICCAT further adopted a rebuilding program for the West Atlantic in which the biomass of adults at maximum sustainable yield is to be attained by 2018 with a 50% or greater probability. The program states that the TAC for this stock should be at 2,500 tonnes (+/- 200 tonnes depending on future SCRS advice).

During the same year, the Commission also set a quota at 32,000 tonnes for the East Atlantic and Mediterranean stock in 1999 (29,500 tonnes in 2000 and 2001). In 2002, it was recommended that bluefin tuna catches should not exceed 32,000 tonnes for the period 2003-2006.

Additionally, an Atlantic-wide size limit of 6.4 kg (i.e. age 2) has been in force since 1975. In 2004, this was raised to 10 kg and 30 kg for the Mediterranean Sea and West Atlantic, respectively. The discrepancy between the minimum sizes between the sides of the ocean occurs because of the disparity in age-at-maturity between the West and East stock and, as well as to differences in the fisheries.

6. Bibliography

ADDIS, P., A. Cau, M. A. Davini, E. Secci and G. Scibaldi. 1997. Collection of tuna data catches by trap-nets in Sardinia: historical (1825-1980) and recent catches (1992-1995). Collect. Vol. Sci. Pap, ICCAT, 46: 132-139.

ARISTOTE. IV B.C., Histoire des animaux. Chapitre 13. Les migrations des poissons. Paris, Gallimard - folio essais.

BARD, F. X. 1981. Le thon germon *Thunnus alalunga* (Bonaterre 1788) de l'océan atlantique. Thèse de Doctorat d'Etat thesis, Université Pierre et Marie Curie, Paris 6, Paris.

BARD, F. X., P. Bach and E. Josse. 1998. Habitat et écophysiologie des thons : Quoi de neuf depuis 15 ans? Collect. Vol. Sci. Pap, ICCAT,50: 319-342.

BERKELEY, S. A., C. Chapman and S. M. Sogard. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, Sebastes melanops. Ecology 85: 1258-1264.

BERTHELOT, S. 1988, Etude sur les pêches maritimes dans la Méditerranée et l'océan. Grenoble, Jean-Pierre Debbane éditeur.

BIGELOW, H. B. and W. C. Schroeder. 1953. Fishes in the Gulf of Maine. Fisheries Bulletin and Wildlife Service 53: 1-577.

BIRKELAND, C. and P. K. Dayton. 2005. The importance in fishery management of leaving the big ones. Trends in Ecology & Evolution 20: 356-358.

BLOCK, B. A., H. Dewar, S. B. Blackwell, T. D. Williams, E. D. Prince, C. J. Farwell, A. Boustany *et al.* 2001. Migratory Movements, Depth Preferences, and Thermal Biology of Atlantic Bluefin Tuna. Science 293: 1310-1314.

BLOCK, B. A., S. L. H. Teo, A. Walli, A. Boustany, M. J. Stokesbury, C. J. Farwell, K. C. Weng et al. 2005. Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434:11211127.

BOUSTANY, A. M., D. J. Marcinek, J. Keen, H. Dewar and B. A. Block. 2001. Movements and temperature preferences of Atlantic bluefin tuna (*Thunnus thynnus*) off North Carolina: A comparison of acoustic, archival and pop-up satellite tags, Pages 89-108 in Sibert, J. R. and J. L. Nielsen, eds. Electronic tagging and tracking in marine fisheries. Dordrecht, Kluwer Academic Publishers.

BRILL, R. W. and M. E. Lutcavage. 2001. Understanding environmental influences on movements and depth distributions of tunas and billfishes can significantly improve population assessments. American Fisheries Society Symposium 25: 179-198.

BRILL, R. W., M. E. Lutcavage, G. Metzger, P. G. Bushnell, M. Arendt, J. Lucy, C. Watson et al. 2001. Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus thynnus*) in relation to oceanographic conditions of the western North Atlantic, determined with ultrasonic telemetry. Fishery Bulletin 100: 155-167.

CARDINALE, M. and F. Arrhenius. 2000. The relationship between stock and recruitment: are the assumptions valid? Marine Ecology Progress Series 196: 305-309.

CARLSSON, J., J. R. McDowell, J. E. L. Carlsson, D. Olafsdottir and J. E. Graves. 2006. Genetic heterogeneity of Atlantic bluefin tuna caught in the eastern North Atlantic Ocean south of Iceland. ICES Journal of Marine Science 63: 1111-1117.

CARLSSON, J., J. R. McDowell, P. Diaz-Jaimes, J. E. L. Carlsson, S. B. Boles, J. R. Gold and J. E. Graves. 2004. Microsatellite and mitochondrial DNA analyses of Atlantic bluefin tuna (*Thunnus thynnus thynnus*) population structure in the Mediterranean Sea. Molecular Ecology 13: 3345-3356.

CATON, A. E. 1991, Review of aspects of southern bluefin tuna biology, population and fisheries. Deriso, R. B. and W. H. Bayliff, eds. World meeting on stock assessment of bluefin tunas: strengths and weaknesses Special Report 7: 181-350.

CETTI, F. 1777, Storia naturale della Sardegna. Sassari., Piattoli.

CHASE, B. C. 2002. Differences in diet of Atlantic tuna (*Thunnus thynnus*) at five seasonal feeding grounds of the New England continental shelf. Fishery Bulletin 100: 168-180.

COLETTE, B. B., C. Reeb and B. A. Block. 2001. Systematics of the tunas and mackerels (scombridae), Pages 1-33 in Block, B. A. and E. D. Stevens, eds. Tuna. Physiology, ecology, and evolution. San Diego, Academic Press.

COMPEAN-JIMENEZ, G. and F. X. Bard. 1980. Age and growth of East Atlantic bluefin tuna as determined by reading of fin rays cross section. Collect. Vol. Sci. Pap, ICCAT, 9: 547-552.

COMPEAN-JIMENEZ, G. and F. X. Bard. 1983. Growth increments on dorsal spines of eastern Atlantic bluefin tuna (*Thunnus thynnus*) and their possible relation to migration patterns, Pages 77-86, NOAA Technical Report. Miami, National Marine Fisheries Service.

CORT, J. L. 1991. Age and growth of the bluefin tuna *Thunnus thynnus* (L.) of the Northeast Atlantic. Collect. Vol. Sci. Pap, ICCAT,35: 213-230.

CURY, P. 1994. Obstinate nature: An ecology of individuals. Thoughts on reproductive behaviour and biodiversity. Canadian Journal of Fisheries and Aquatic Science 51: 1664-1673.

DE BUEN, F. 1925. Biologia del atun (*Orcynnus Thynnus L.*). Resultado Campañas Realizadas por Acuerdos Internacionales bajo la Direccion del Prof. de Buen, Pages 1-118. Madrid, Ministerio de Marina-Direccion General de Pesca.

DE LA SERNA, J. M., J. M. Ortiz de Urbina and E. Alot. 2003. Analysis of sex-ratio by length-class for bluefin tuna (*Thunnus thynnus*) in the western Mediterranean and eastern Atlantic. Collect. Vol. Sci. Pap, ICCAT, 55: 166-170.

DE METRIO, G., G. P. Arnold, B. A. Block, J. M. de la Serna, M. Deflorio, M. Cataldo, C. Yannopoulos et al. 2002. Behaviour of post-spawning Atlantic bluefin tuna tagged with pop-up satellite tags in the Mediterranean and eastern Atlantic. Collect. Vol. Sci. Pap, ICCAT, 54: 415-424.

DESSE, J. and N. Desse-Berset. 1994. Stratégies de pêche au 8ème millénaire : les poissons de Cap Andreas Kastros (Chypre), Pages 335-360 in Le Brun, A., ed. Fouilles récentes à Khirokitia. Paris, Editions Recherche sur Civilisations.

DIAZ, G. and Turner S. 2007. Size frequency distribution and age estimation of BFT in the Gulf of Mexico during the spawning season. Collect. Vol. Sci. Pap, ICCAT, (in press).

DOUMENGE, F. 1998. L'histoire des pêches thonières. Collect. Vol. Sci. Pap, ICCAT, 50: 753-803.

DOUMENGE, F. 2000. La pêche en Méditerranée, Pages 42 pp. Palavas-Les-Flots (France), Centre d'Etudes et de Rencontres Méditerranéennes (CERM).

EGGLESTON, D. B. and E. A. Bochenek. 1990. Stomach contents and parasite infestation of school bluefin tuna *Thunnus thynnus* collected from the Middle Atlantic Bight, Virginia. Fisheries Bulletin 88: 389-395.

ELY, B., D. S. Stoner, J. M. Dean, J. R. Alvarado Bremer, S. Chow, S. Tsuji, T. Ito *et al.* 2002. Genetic analyses of Atlantic northern bluefin tuna captured in the northwest Atlantic Ocean and the Mediterranean Sea. Collect. Vol. Sci. Pap, ICCAT, 54: 372-376.

EVENSON, J. P., G. M. Laslett and T. Polacheck. 2004. An integrated model for growth incorporating tag-recapture, length-frequency and direct ageing data. Canadian Journal of Fisheries and Aquatic Science 61: 292-306.

FARLEY, J. H. and T. L. O. Davis. 1998. Reproductive dynamics of southern bluefin tuna, *Thunnus maccoyii*. Fishery Bulletin 96: 223-236.

FARRUGIO, H. 1981. Exploitation et dynamique des populations de thon rouge, *Thunnus thynnus* (Linné 1758), Atlanto-Méditérranéennes. Doctorat d'Etat thesis, Université des Sciences et Techniques du Languedoc, Montpellier.

FROMENTIN, J.-M. 2003. Why uncertainty in the management of the East Atlantic Bluefin tuna has constantly increased in the past few years. Scientia Marina 67: 51-62.

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

FROMENTIN, J.-M. and J. E. Powers. 2005. Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. Fish and Fisheries 6: 281-306.

FROMENTIN, J.-M. and C. Ravier. 2005. The East Atlantic and Mediterranean bluefin tuna stock: looking for sustainability in a context of large uncertainties and strong political pressures. Bulletin of Marine Science 76: 353-362.

GUNN, J. and B. A. Block. 2001. Advances in acoustic, archival, and satellite tagging of tunas, Pages 167-224 in Block, B. A. and E. D. Stevens, eds. Tuna. Physiology, ecology, and evolution. San Diego, Academic Press.

HAMRE, J., F. Lozano, J. Rodriguez-Roda and K. Tiews. 1968. Report from the bluefin tuna working group, Pages 27p. Copenhagen, Conseil Permanent international pour l'Exploration de la Mer.

HATTOUR, A. 2003. Analyse du sex ratio par classe de taille du thon rouge (*Thunnus thynnus*) capturé par les senneurs tunisiens. Collect. Vol. Sci. Pap, ICCAT, 55: 232-237.

HELDT, M. H. 1929. Le thon rouge et sa peche. Rapport et Procès-verbaux des Réunions de la Commission internationale de l'Exploration Scientifique de Mer Méditerranée 4: 97-112.

HUMSTON, R., J. S. Ault, M. Lutcavage and D. B. Olson. 2000. Schooling and migration of large pelagic fishes relative to environmental cues. Fisheries Oceanography 9: 136-146.

ICCAT. 1984. Report of the bluefin tuna workshop, Japan September 1983. Collect. Vol. Sci. Pap, ICCAT, 19:1-282.

ICCAT. 1997. 1996 SCRS Detailed Report on Bluefin Tuna. Collect. Vol. Sci. Pap, ICCAT, 46: 1-301.

ICCAT. 1999. 1998 SCRS Detailed Report on Bluefin Tuna. Collect. Vol. Sci. Pap, ICCAT, 49: 1-191.

ICCAT. 2002a. ICCAT Workshop on Bluefin Tuna Mixing. Collect. Vol. Sci. Pap, ICCAT, 54: 261-352.

ICCAT. 2002b. Report of the ICCAT Workshop on environment and tuna recruitment (Madrid, Spain, May 7-12, 2001). Collect. Vol. Sci. Pap, ICCAT, 54: 895-952.

ICCAT. 2003a. Report of the 2002 Atlantic Bluefin Tuna Stock Assessment Session. Collect. Vol. Sci. Pap, ICCAT, 55: 710-937.

ICCAT. 2003b. Report of the Sixth GFCM-ICCAT Meeting on Stocks of Large Pelagic Fishes in the Mediterranean. Collect. Vol. Sci. Pap, ICCAT, 55: 1-84.

ICCAT. 2005. Report of the 2004 data exploratory meeting for the East Atlantic and Mediterranean bluefin tuna. Collect. Vol. Sci. Pap, ICCAT, 58: 662-699.

ICCAT. 2007. Report of the 2006 Atlantic Bluefin Tuna Stock Assessment Session. Collect. Vol. Sci. Pap, ICCAT, 64: 652-880.

ICCAT. 2008. Statistical Bulletin Vol. 37. 194 pp.

INAGAKE, D., H. Yamada, K. Segawa, M. Okazaki, A. Nitta and T. Itoh. 2001. Migration of young bluefin tuna, *Thunnus orientalis* Temminck et Schlegel, through archival tagging experiments and its relation with oceanographic conditions in the Western North Pacific. Bulletin of Natural Resource Institut of the Far Seas Fisheries 38: 53-81.

KARAKULAK, S., I. Oray, A. Corriero, A. Aprea, D. Spedicato, D. Zubani, N. Santamaria et al. 2004. First information on the reproductive biology of the bluefin tuna (*Thunnus thynnus*) in the eastern Mediterranean. Collect. Vol. Sci. Pap, ICCAT, 56: 1158-1162.

KELL, L. T., D. Die, V. Restrepo, J.-M. Fromentin, V. Ortiz de Zarate and P. Pallares. 2003. An evaluation of management strategies for Atlantic tuna stocks. Scientia Marina 67: 53-370.

LABELLE, M., T. Hoch, B. Liorzou and J. L. Bigot. 1997. Indices of bluefin tuna (*Thunnus thynnus thynnus*) abundance derived from sale records of French purse seine catches in the Mediterranean Sea. Aquatic Living Resources 10: 329-342.

LAURS, R. M., P. C. Fiedler and D. R. Montgomery. 1984. Albacore tuna catch distributions relative to environmental features observed from satellites. Deep Sea Research 31: 1085-1099.

LEHODEY, P., M. Bertignac, J. Hampton, A. Lewis and J. Picaut. 1997. El Nino Southern Oscillation and tuna in the western Pacific. Nature 389: 715-718.

LUTCAVAGE, M., R. W. Brill, G. B. Skomal, B. C. Chase and P. W. Howey. 1999. Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? Canadian Journal of Fisheries and Aquatic Science 56: 173-177.

LUTCAVAGE, M. E., R. W. Brill, G. B. Skomal, B. C. Chase, J. L. Goldstein and J. Tutein. 2000. Tracking adult North Atlantic bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic using ultrasonic telemetry. Marine Biology 137: 347-358.

LUTCAVAGE, M. E., Brill, R. W., Porter, J. M. *et al.* (2001) Summary of the pop-up satellite tagging of giant bluefin tuna in the joint US-Canada program, Gulf of Maine and Canadian Atlantic. Collect. Vol. Sci. Pap, ICCAT, 52: 759-770.

MARSAC, F. 1999. Changements hydroclimatiques observés dans l'Atlantique depuis les années 50 et impacts sur quelques stocks de thons et leur exploitation. Collect. Vol. Sci. Pap, ICCAT, 49: 346-370.

MARTEINSDOTTIR, G. and G. A. Begg. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod Gadus morhua. Marine Ecology Progress Series 235: 235-256.

MATHER, F. J., J. M. Mason Jr and A. Jones. 1995. Historical document: life history and fisheries of Atlantic bluefin tuna, Pages 165 pp. Miami, NOAA Technical Memorandum NMFS-SEFSC-370.

MEDINA, A., F. J. Abascal, C. Megina and A. García. 2002. Stereological assessment of the reproductive status of female Atlantic northern bluefin tuna during migration to Mediterranean spawning grounds through the Strait of Gibraltar. Journal of Fish Biology 60: 203-217.

MEYER-WAARDEN, P. F. 1959. Relation between the tuna populations of the Atlantic, Mediterranean and North Seas. Proceedings of the general Fisheries Council of the Mediterranean 5: 197-202.

MUSYL, M. K., R. W. Brill, C. H. Boggs, D. S. Curran, T. K. Kazama and M. P. Seki. 2003. Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. Fisheries Oceanography 12: 152-169.

NISHIKAWA, Y., M. Honma, S. Ueyanagi and S. Kikawa. 1985. Average distribution of larvae of oceanic species of scombroid species, 1956 - 1981. Far Seas Fisheries Research Laboratory Serie S 12:99 pp.

NORTARBARTOLO DI SCIARA, G. 1987. Killer whale, Orcinus orca, in the Mediterranean Sea. Marine Mammal Science 3: 356-360.

ORTIZ DE ZARATE, V. and J. L. Cort. 1986. Stomach contents study of immature bluefin tuna in the Bay of Biscay. ICES-CM H: 26:10 pp.

PARRACK, M. and P. Phares (1979) Aspects of the growth of Atlantic bluefin tuna determined from markrecapture data. ICCAT Collective Volume of Scientific Papers, 8: 356-366.

PAVESI, P. 1889, L'industria del tonno. Roma, Relatione alla commissione reale per le tonnare, Ministero di Agricultura, Industria e Commercio.

PICINETTI, C. and G. Piccinetti Manfrin. 1993. Distribution des larves de thonidés en Mediterranée. Collect. Vol. Sci. Pap, ICCAT, 40: 164-172.

PLINE, l. a. Ith A.C., Histoire Naturelle. Livre IX. Paris, Les Belles Lettres.

PORCH, C. E. 2005. The sustainability of Western Atlantic bluefin tuna: A warm blooded fish in a hot blooded fishery. Bulletin of Marine Science 76: 363-384.

PORCH, C. E., S. C. Turner and J. E. Powers. 2001. Virtual population analyses of Atlantic bluefin tuna with alternative models of transatlantic migration: 1970-1997. Collect. Vol. Sci. Pap, ICCAT, 52: 1022-1045.

POWERS, J. E. and J. Cramer. 1996. An exploration of the nature of Atlantic bluefin tuna mixing. Collect. Vol. Sci. Pap, ICCAT, 45: 173-181.

POWERS, J. E. and Porch, C. E. (2004). Approaches to developing management procedures which incorporate mixing. Collect. Vol. Sci. Pap, ICCAT, 56: 1144-1152.

PUJOLAR, J. M. and C. Pla. 2000. Genetic differentiation between north-west Atlantic and Mediterranean samples of bluefin tuna (*Thunnus thynnus*) using isozyme analysis. Collect. Vol. Sci. Pap, ICCAT, 51: 882 - 891.

PUSINERI, C., C. Ravier and J.-M. Fromentin. 2002. Retrospective analysis of the bluefin tuna Nordic fisheries data. Collect. Vol. Sci. Pap, ICCAT, 54: 517-526.

RAVIER, C. and J.-M. Fromentin. 2001. Long-term fluctuations in the Eastern Atlantic and Mediterranean bluefin tuna population. ICES Journal of Marine Science 58: 1299-1317.

RAVIER, C. and J.-M. Fromentin. 2002. Eastern Atlantic bluefin tuna: what we learnt from historical time-series of trap catches. Collect. Vol. Sci. Pap, ICCAT, 54: 507-516.

RAVIER, C. and J.-M. Fromentin. 2004. Are the long-term fluctuations in Atlantic bluefin tuna (*Thunnus thynnus*) population related to environmental changes? Fisheries Oceanography 13: 145-160.

RODRIGUEZ-RODA, J. 1964. Biologia del Atun, *Thunnus thynnus* (L.), de la costa sudatlantica de Espana. Investigacion Pesqua 25: 33-146.

RODRIGUEZ-RODA, J. 1967. Fecundidad del atun, *Thunnus thynnus* (L.), de la costa sudatlantica de España. Investigacion pesquera 31: 35-52.

ROOKER, J. R. and D. H. Secor. 2004. Stock structure and mixing of Atlantic bluefin tuna: Evidence from stable d13C and d18O isotopes in otoltihs. Collect. Vol. Sci. Pap, ICCAT, 56: 1115-1120.

ROOKER, J. R., D. H. Secor, V. S. Zdanowicz, G. De Metrio and L. Orsi-Relini. 2003. Identification of Atlantic bluefin tuna (*Thunnus thynnus*) stocks from putative nurseries using otolith chemistry. Fisheries Oceanography 12: 75-84.

ROOKER, J. R., D. H. Secor, V. S. Zdanowicz, G. De Metrio, L. Orsi Relini, M. Deflorio, G. Palandri *et al.* 2002. Otolith elemental fingerprints of Atlantic bluefin tuna from Eastern and Western nurseries. Col. Vol. Sci. Pap. ICCAT.

ROULE, L. 1917. Etude sur les aires de ponte et les déplacements périodiques du thon (*Orcynus thunnus L.*) dans la Méditerranée occidentale. Annales de l'Institut Océanographique 7: 1-26.

ROYER, F., J.-M. Fromentin and P. Gaspar. 2004. The association between bluefin tuna schools and oceanic features in the Western Mediterranean Sea. Marine Ecology Progress Series 269: 249-263.

SARA, R. 1969. La pesca del tonno in Tirreno nel 1969. Bollettino di Pesca, Piscicultura e Idrobiologia, Roma 24: 217-243.

SCHAEFER, K. M. 2001. Reproductive biology of tunas, Pages 225-270 in Block, B. A. and E. D. Stevens, eds. Tuna. Physiology, ecology, and evolution. San Diego, Academic Press.

SCHICK, R. S., J. Goldstein and M. E. Lutcavage. 2004. Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994-96). Fisheries Oceanography 13: 225-238.

SELLA, M. 1929. Migrazioni e habitat del tonno (*Thunnus thynnus, L.*) studiati col metodo degli ami, con osservazioni su l'accrescimento, sul regime delle tonnare ecc. Memoria R. Comitato Talassografico Italiano Memoria 156:511-542.

SUSCA, V., A. Corriero, M. Deflorio, C. R. Bridges and G. De Metrio. 2001. New results on the reproductive biology of bluefin tuna (*Thunnus thynnus*) in the Mediterranean. Collect. Vol. Sci. Pap, ICCAT, 52:7 45-751.

TIEWS, K. 1957. Biologische untersuchungen am roten thun (*Thunnus thynnus* L.) in der Nordsee. Berichte der Deutschen Wissenschaftlichen Komission Fur Meeresfsorschung, Stuggart 14: 192-220.

TIEWS, K. 1963. An attempt to estimate the rate of transatlantic exchange of large bluefin tuna from German tuna catches by means of the feeding condition factor K. Int. Counc. Explor. Sea. Ann. Biol. 19: 183-184.

TIEWS, K. 1978. On the disapperance of bluefin tuna in the North Sea and its ecological implications for herring and mackerel. Rapport et Procès-verbaux des Réunions du Conseil international de l'Exploration de la Mer 172: 301-309.

TURNER, S. C., V. R. Restrepo and A. M. Eklund. 1991. A review of the growth rate of West Atlantic bluefin tuna, *Thunnus thynnus*. Collect. Vol. Sci. Pap, ICCAT, 35: 271-293.

TURNER, S. C. and V. R. Restrepo. 1994. A review of the growth rate of West Atlantic bluefin tuna, *Thunnus thynnus*, estimated from marked and recaptured fish. Collect. Vol. Sci. Pap. ICCAT, 42: 170-172.

UOTANI, I., T. Saito, K. Hiranuma and Y. Nishikawa. 1990. Feeding habit of bluefin tuna *Thunnus thynnus* larvae in the western North Pacific Ocean. Bulletin of the Japanese Society of Science and Fisheries 56: 713-717.

VETTER, E. F. 1987. Estimation of natural mortality in fish stocks: a review. Fisheries Bulletin 86:25-43.

VIÑAS, J., C. Pla, M. El Tawil, A. Hattour, A. F. Farrugia and J. M. de la Serna. 2003. Mitochondrial genetic characterization of bluefin tuna (*Thunnus thynnus*) from three Mediterranean (Libya, Malta, Tunisia); and one Atlantic locations (Gulf of Cadiz). Collect. Vol. Sci. Pap, ICCAT, 55:1282-1288.

WILSON, S. G., M. E. Lutcavage, R. W. Brill, M. P. Genovese, A. B. Cooper and A. W. Everly. 2005. Movements of bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic Ocean recorded by pop-up satellite archival tags. Marine Biology 146:409-423.