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Atlantic bluefin tuna: population dynamics, ecology, fisheries and management

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Abstract: Both old and new information on the biology and ecology of Atlantic bluefin tuna have confronted scientists with research challenges: research needs to be connected to current stock-assessment and management issues. We review recent studies on habitat, migrations and population structure, stressing the importance of electronic tagging results in the modification of our perception of bluefin tuna population dynamics and behaviour. Additionally, we question, from both scientific and management perspectives, the usefulness of the classical stock concept and suggest other approaches, such as Clark's contingent and metapopulation theories. Current biological information confirms that a substantial amount of uncertainty still exists in the understanding of reproduction and growth. In particular, we focus on intriguing issues such as the difference in age-at-maturity between West Atlantic and Mediterranean bluefin tuna. Our description of Atlantic bluefin tuna fisheries places today's fishing patterns within the two millennium history of exploitation of this species: we discuss trap fisheries that existed between the 17th and the early 20th centuries; Atlantic fisheries during the 1950s and 1960s; and the consequences of the recent development of the sushi–sashimi market. Finally, we evaluate stock status and management issues since the early 1970s. While important uncertainties remain, when the fisheries history is confronted with evidence from biological and stock-assessment studies, results indicate that Atlantic bluefin tuna has been undergoing heavy overfishing for a decade. We conclude that the current exploitation of bluefin tuna has many biological and economic traits that have led several fish stocks to extreme depletion in the past.

Keywords: Atlantic-bluefin-tuna; population-dynamics; population-structure; stock-assessment-and-management; Thunnus-thynnus; tuna-fisheries

Introduction

Atlantic bluefin tuna (*Thunnus thynnus*, Scombridae) have fascinated scientists and philosophers for centuries, starting with the ancient Greek and Latin philosophers (Aristotle and Pliny the Elder) and continuing with many scientists since the end of the 18th century. This fascination comes from striking biological properties, such as an impressive size (> 3 m and up to 900 kg) and a swimming speed which allows extensive migrations between cold temperate feeding grounds and warm waters spawning grounds. The Atlantic bluefin tuna (ABFT) has also been of great economic interest, as it has been continually and significantly exploited in the Mediterranean Sea for thousands of years (Mather *et al.* 1995; Doumenge 1998). Presently, ABFT is back in the limelight, as fishing for it has become a highly profitable activity particularly with the development of the sushi-sashimi in Japan. This new market opportunity has increased demand for high quality fish, stimulating the market to attain some very high prices in recent years. For example, a single bluefin tuna was sold for 174,000 US$ in 2001 at the Tokyo market. This new situation has inevitably induced tension between various fishing entities, including fishermen, national and international administrations, national scientists and NGOs (Fromentin and Ravier 2004; Porch 2005).

While remarkable changes have occurred in the exploitation of ABFT during the last two decades, research activities have also been vigorous during that period. The physiology, biology and behaviour of this species is somewhat better understood. For example, since ABFT is a pelagic fish that never stops swimming to ventilate (like other tunas and some sharks), it continuously generates heat which is used to elevate and maintain muscle, eye, brain and visceral temperatures above water temperatures. This property of endothermy is highly developed in ABFT and contributes to its extensive capacity for migration (for a recent review see Graham and Dickson 2001). Also, our perception of population and spatial dynamics has been strongly modified by recent studies on biology and ecology of ABFT (e.g., Humston *et al.* 2000; Ravier and Fromentin 2001; Medina *et al.* 2002; Rooker *et al.* 2003; Carlsson *et al.* 2004; Royer *et al.* 2004), electronic tagging experiments (see e.g., Lutcavage *et al.* 2000; Block *et al.* 2001; Gunn and Block 2001) and new modelling approaches (Punt and Butterworth 1995; Porch *et al.* 2001).

Nevertheless, linkages between advances in biology and ecology of ABFT and current developments in fisheries biology, exploitation and management are still lacking. The last extensive review of ABFT was published by Mather *et al.* (1995). Note that despite the relatively recent date of publication, this review was prepared during the 1970s (more than 25 years ago). Nevertheless, it remains a key reference. Thus, there is a need to examine more recent research activities. The purpose of this article is to review key information on ABFT (both old and new) and to link major research results with stock assessment and management challenges, in order to provide an overall characterization of this species and its exploitation.

Ecology and Population structure

Habitat

Atlantic bluefin tuna inhabit the pelagic ecosystem of the entire North Atlantic and its adjacent seas, primarily the Mediterranean Sea (i.e. from the equator to the North of Norway and from the Black Sea to the Gulf of Mexico ((Mather *et al.* 1995). Among the tuna, ABFT 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 ABFT can sustain cold (down to 3°C) as well as warm (up to 30°C) temperatures while maintaining stable internal body temperature (Block *et al.* 2001). Until recently, it was assumed that ABFT preferentially occupies the surface and subsurface waters of the coastal and open-sea areas, but archival tagging and ultrasonic telemetry have changed our perception. While ABFT appear to primarily reside in surface waters, both juveniles and adults ABFT frequently dive to depth of 500m to 1000m (Lutcavage *et al.* 2000; Block *et al.* 2001; Brill *et al.* 2001). Similar behaviour has also been reported for southern bluefin tuna, bigeye tuna and swordfish and is generally related to foraging in deep scattering layers and/or to physiological constraints to cool the body temperature (Carey and Robinson 1981; Holland *et al.* 1992; Bard *et al.* 1998; Gunn and Block 2001; Musyl *et al.* 2003). These results make clear that the habitat of ABFT cannot be solely described in two dimensions (Brill and Lutcavage 2001; Wilson *et al.* 2005).

Figure 1, about here

The spatial distribution and movement of ABFT are hypothesized to be controlled by preferential ranges and gradients of temperature (see e.g., Roffer 1987), similar to Pacific bluefin and other tuna species (Laurs *et al.* 1984; Lehodey *et al.* 1997; Bard 2001; Inagake *et al.* 2001). However, ABFT's high vertical mobility makes this species less likely to detect horizontal thermal gradients (as vertical temperature gradients are much larger than horizontal ones, see Brill and Lutcavage 2001; Brill *et al.* 2001). More recent work appears to converge toward the opinion that juvenile and adult ABFT frequent and aggregate along ocean fronts (Humston *et al.* 2000; Lutcavage *et al.* 2000; Royer *et al.* 2004). This association is also likely to be related to foraging, ABFT feeding on the abundant vertebrate and invertebrate prey concentrations of these areas (e.g., Boustany *et al.* 2001; Brill *et al.* 2001). The types of ocean fronts known to be frequently visited by ABFT 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 (e.g., the East coast of North America from Cape Hatteras to the Gulf of St Lawrence, the Bay of Biscay and the northwestern Mediterranean, Farrugio 1981; Mather *et al.* 1995; Bard *et al.* 1998; Boustany *et al.* 2001; Wilson *et al.* 2005). Despite this general agreement, the habitat of ABFT 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).

Migration and stock delimitation

Intrigued by the seasonal appearance of ABFT in various parts of the Mediterranean Sea, the ancient Greek and Latin philosophers, Aristotle (IV Century B.C.) and Pliny the Elder (I Century A.D.), speculated that ABFT migrate close to the coasts by keeping the shore on their right and so, perform a large anti-cyclonic movement all around the Mediterranean. A migratory connection between oceans was first mentioned by Cetti (1777), who suggested that ABFT come into the Mediterranean from the North Atlantic to spawn around Sicily (either by following the North African or the European coasts) and then go back (by the same routes). Through observation of Italian trap fisheries, Pavesi (1889) disagreed with Cetti and postulated the occurrence of a separate Mediterranean ABFT stock. Surprisingly, his hypothesis, known as the ‘native hypothesis’, remained dominant for several decades and was accepted by several authors (e.g., Roule 1917; de Buen 1925; Scordia 1938). The native hypothesis was finally questioned when some hooks used in the North Atlantic (which were sufficiently different from ones used in the Mediterranean) 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 ((see “Stock Status and Management” section or Sara 1963; Mather *et al.* 1995).

Migration between the North Atlantic and the Mediterranean has been documented by many observations since then. These observations have also led to the hypothesis that ABFT display a homing behaviour, i.e. that ABFT migrate to spawn in specific and well defined areas (Figure 1). This hypothesis is supported by the most extensive electronic study published to date (Block *et al.* 2005), which tends to support spawning site fidelity in both the Mediterranean Sea and Gulf of Mexico. Furthermore, ABFT distribute themselves over a wide habitat (probably at a rather low density), so that aggregation of individuals at any given time and place appears necessary to ensure mating and reproduction success of the population (e.g., Sinclair 1988). Ecologists usually distinguish between natal homing (a strict fidelity to the birth location due to imprinting of environmental cues during early life stages, such as salmon, Cury 1994; Dittman and Quinn 1996) and repeat homing (a process related to spatial learning of the younger from the older individuals, Dodson 1988). Dodson (1988) and McQuinn (1997) also argued that spatial learning would be advantageous when fish can repeat experiences (i.e. iteroparous reproduction) and when they live in unstable and unpredictable environments (such as oceanic ones where the probability of recruitment failures are high). Conversely, imprinting would be beneficial to a semelparous reproductive strategy (e.g. salmon), especially in relatively stable environments (such as rivers). So in theory, ABFT is more likely to perform repeat homing, which is in further agreement with several observations and findings. Indeed, the schools of migrating spawners include a broad range of individual sizes (and ages) and their quantity seem to fluctuate in relation to environmental conditions (Ravier and Fromentin 2004). Furthermore, past works have mentioned other spawning locations than are believed to occur today (see also the “Reproduction” section), which could be due to the disappearance of some spawning habitats or to shifts of preferences for some areas to others.

Figure 2, about here

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 ABFT vary considerably between individuals, years and areas (Lutcavage *et al.* 1999; Block *et al.* 2001; Lutcavage *et al.* 2001; de Metrio *et al.* 2002). The appearance and disappearance of past fisheries also suggest that important changes in the spatial dynamics of

ABFT may be environmentally driven (Marsac 1999; Ravier and Fromentin 2004). After examining size composition of the ABFT 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 (Figure 2). Indeed, the mean size of ABFT caught by the Norwegian fleet continuously increased after the collapse of fishing in 1963. The size composition of the catch included fish from 140 to 250 cm (i.e. 50-200kg) during the 1950s; then the size composition was solely comprised of fish > 240 cm during the 1970s (> 200kg, see Figure 3). Pusineri et *al.* (2002) showed that catch compositions dominated by older ages occurred during the same period in the main Spanish trap, suggesting that the East Atlantic and Mediterranean ABFT might have suffered poor recruitment years (perhaps driven by environmental changes and/or by overfishing). Alternatively, there may have been changes in migration patterns as suggested by Tiews (1978). A quick examination of data from the ABFT bait boat fishery in the Bay of Biscay (which only targets juveniles fish) does not indicate any recruitment failure during the 1960s. However, a more extensive analysis of the catch composition of the most important Atlantic and Mediterranean fisheries operating from the 1950s to the 1970s would be necessary to discriminate between these hypotheses.

Changes in migration patterns might also be the cause of the “Brazilian episode”. This episode was a short period from 1962 to 1967 during which Japanese longliners caught 5,000 to 12,000 tonnes of ABFT in an area where they usually caught tropical tuna (Figure 2). Although the onset of the Brazilian episode coincides with the collapse of the Nordic fisheries, no clear link between the two has been established. Perhaps, the collapse of fishing in these two distant areas might have been due to overfishing on local (possibly isolated) populations of ABFT. However, in the case of the Brazilian episode, questions remain as to how a long-lived fish such as ABFT could have been fished out within 6 years by a relatively few number of longliners.

Figure 3, about here

Isolated populations or Metapopulations?

Understanding the dynamics and spatial distribution of ABFT is crucial for management, as spatial variability governs the definition of management units, stocks and boundaries. The International Commission for the Conservation of Atlantic Tunas (ICCAT) currently manages ABFT as two stocks with the boundary between the two spatial units being the 45°W meridian (Figure 1). This delimitation was originally established for management convenience (for more details, see “Stock Status and Management” section). But with the accumulation of observations from electronic tagging this management structure has been strongly criticised, as higher rates of trans-Atlantic migration than previously suspected have been detected (Lutcavage *et al.* 1999; Block *et al.* 2001). Based on an impressive and unique tagging effort (772 electronic tags being deployed), (Block *et al.* 2005) advocated for the two ABFT populations hypothesis, each with its distinct spawning area (i.e. the Mediterranean Sea and the Gulf of Mexico), but with an overlapping distribution on North Atlantic feeding grounds. This hypothesis (which is certainly the best documented to date) implies that substantial changes in ICCAT management delimitations might be in order (see below ‘Management Section’). However, the major difficulty with electronic tagging relates to the representativeness of the sampled fish to the ABFT population as a whole. The last stock size estimate indicated that ABFT populations still include several million fish (ICCAT 2003b). Thus, even with the large number of electronic tags used to date, it is unclear if all of the modes of ABFT behaviour are represented in the sample. Additionally, variability in trans-Atlantic migration rates inferred from conventional tagging studies appear to fluctuate greatly between years or decades (~7.6% in the 1990s, ~1.2% in 1980s, <1% in the 1970s and ~2.3%

in the 1960s, Fromentin 2002a). Therefore, obtaining a representative sample of electronic tagged fish may be out of reach at current costs. This makes the population migration rates still difficult to quantify from either traditional or electronic tagging (Porch *et al.* 2001).

Additionally, electronic tagging does not provide the location of birth of the migrating fish, a key information needed for understanding the population structure. To get this critical information, chemical signatures in hard structures of teleost fish (that represent natural tags) might help (Secor *et al.* 2002). Measuring the concentration of 6 elements (Li, Mg, Ca, Mn, Sr and Ba), Rooker *et al.* (2003) showed that the otolith chemistry of ages-0 and -1 ABFT collected from the Mediterranean Sea and Gulf of Mexico nurseries could be distinguished (note that the three Mediterranean nursery areas included in the study also displayed distinct differences). Using alternative geochemical markers (especially stable d18O isotope), Rooker and Secor (2004) could further discriminate otoliths chemistry from medium- and large-size ABFT. The presence of genetic stock structure in ABFT populations has also been investigated using microsatellite and mitochondrial DNA or isozymes (Broughton and Gold 1997; Pujolar and Pla 2000; Viñas *et al.* 2001; Ely *et al.* 2002; Viñas *et al.* 2003; Carlsson *et al.* 2004). However, results are not yet conclusive and remain somewhat controversial. For example, Viñas *et al.* (2001; 2003) concluded that no genetic differences could be detected within Mediterranean ABFT, whereas Carlsson *et al.* (2004) reached the opposite conclusion. Such differences probably result from some discrepancies in the sampling design and/or markers used. Genetic and microchemistry analyses are undoubtedly very promising and should be extended, but, in the case of ABFT population structure, genetic analyses need to be standardized to avoid conflicting results.

Alternatively, one begins to question the concept of a stock, itself, where populations are assumed to be both reproductively and geographically isolated. The traditional unit stock approach is related to discrete population concepts or the migrant/vagrant hypothesis (e.g., Sinclair and Iles 1989). However, another approach, based on the concept ‘density-dependent habitat selection’ (MacCall 1990), might be more appropriate. Under the latter view, ABFT might be comprised of several groups of individuals which congregate at a certain spatial scale for reproduction, but whose population-level spatial range might expand and contract in response to both environmental and fishing variability (e.g., Smith and Jamieson 1986). However, neither of these two theories fully succeeds in explaining concomitant variability in migration patterns or the colonization and extinction of local populations in some areas *versus* the strong persistence of specific spawning grounds and migration routes. Recent studies on salmon, herring and striped bass have opened new avenues for interpreting the complexity of fish dynamics that appear more appropriate. For example, concepts of imprinting and Clark‘s contingent definition purport that divergent energy allocations during early life stages can cause divergent migration or habitat uses among groups of fish (Clark 1968; Secor 1999). These differences could further persist in case of reproductive isolation, phenotypic plasticity and/or heterogeneous distribution of the habitat. An alternative approach follows the concept of metapopulation theory from which ABFT would be seen as a collection of discrete local populations, occupying distinct and patchy suitable habitats, displaying their own dynamics but with a degree of demographic influence from other local populations through dispersal (Levins 1969; Hanski 1999; Kritzer and Sale 2004). Within each local population, individuals would display similar migration or habitat uses, resulting from a common spatial learning among individuals (Slatkin and Wade 1978; Olivieri *et al.* 1990; McQuinn 1997). Both hypotheses might provide a better explanation of the concomitance of homing behaviour with the occurrence of colonization and extinction in some areas. The main difference between Clark’s contingent hypothesis and the metapopulation approach finally lies with the importance given to the deterministic (imprinting) *versus* stochastic (behavioural) processes. More likely, there is no single factor but rather a mixture of mechanisms acting in ABFT populations. This issue is fascinating from an ecological viewpoint and is crucial for management, as the effects of exploitation and the potential of the population to recover from overfishing depend on the ecological processes which are in effect.

Biology

Maturity

Past studies have found that *Thunnus thynnus* mature at approximately 4 years of age for the East Atlantic and Mediterranean Sea, but at around 8 years for the West Atlantic (length at maturity is about 110-120cm (30-35 kg) *versus* about 200cm (150 kg), respectively, (see Mather *et al.* 1995, for a review). This disparity between the two sides of the North Atlantic 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 ABFT (from 8 to 12 years depending on the authors, Caton 1991; Schaefer 2001). Comparing information on reproductive biology of tuna, Schaefer (2001) recently stressed the limited amount of information on size and/or age-at-maturity and the lack of valid histological criteria for this species. Subsequent to that investigation, new studies have been carried out in various areas of the Mediterranean Sea (ICCAT 2003c). Further progress has been made in the determination of maturity by measuring hormone concentrations in blood (Susca *et al.* 2001). All these studies have confirmed past estimates, i.e. length at maturity at around 120 cm for female ABFT in the Mediterranean Sea. Differences in age-at-maturity between West Atlantic and Mediterranean ABFT might support the discrete population hypothesis (i.e. two stocks), but this remains rather puzzling given the apparent level of mixing. Further investigation is needed. A prerequisite would be to carry out extensive trans-Atlantic surveys to study maturity of ABFT using the same sampling protocol throughout the Atlantic and Mediterranean (see “Perspectives” section).

Reproduction

As all tuna species, bluefin tuna is oviparous and iteroparous (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). Like most fish, egg production appears to be 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 ABFT (Farley and Davis 1998; which is comparable to that found for other tuna Schaefer 2001; Medina *et al.* 2002). The conventional assumption still is that adult ABFT spawn each year. However, electronic tagging experiments have shown that adult-sized fish have occurred some distance from any known spawning ground during the spawning season (Lutcavage *et al.* 1999). Also, experiments in captivity (Lioka *et al.* 2000) raise questions about this assumption and suggest that spawning by an individual might occur only once every two or three years.

The location of spawning sites have been determined by either noting the location of fish with the appropriate gonadal condition or by noting the distribution of larvae. Although both methods are subject to limitations (Schaefer 2001), it is generally agreed that ABFT spawning takes place in warm waters (greater than 24°C) of specific and restricted locations (around the Balearic islands, Sicily and the Gulf of Mexico, Figure 1) and occurs only once a year (around May and June for the West and East Atlantic, respectively, Nishikawa *et al.* 1985; Mather *et al.* 1995; Schaefer 2001). In contrast with tropical tuna which spawn and feed throughout the tropical and subtropical oceans, ABFT appear to 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 (Picinetti and Piccinetti Manfrin 1993; Mather *et al.* 1995). Picinetti and Picinetti-Manfrin (1993), who conducted egg and larvae surveys over the entire Mediterranean Sea between 1977 and 1988, concluded that spawning locations of ABFT were more distributed than usually accepted, extending into the Eastern Mediterranean Sea. A recent larval survey tends to confirm this (Karakulak *et al.* 2004). Electronic tagging experiments have further raised the possibility of ABFT spawning in the mid-Atlantic (Lutcavage *et al.* 1999). However, this has not been confirmed by recent larval surveys. Whatsoever, it appears that our understanding of ABFT spawning locations still remains incomplete.

ABFT appear to spawn when they reached specific locations (Rodriguez-Roda 1964; 1967), which has been supported by recent studies (Medina *et al.* 2002). These authors showed that very rapid gonadal maturity occurs between the time the migrating fish are caught in the Strait of Gibraltar and the fish spawn in the Balearic area a few weeks later. This rapid gonadal development is possibly influenced by increasing water temperature. Spawning fertilization occurs directly in the water column and hatching happens without parental care after an incubation period of 2 days. 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, then the larvae have to feed on their own. The age-structure of the spawning stock and the condition of the spawners of ABFT may affect the reproductive potential and viability of offspring as has been shown for some groundfish and rockfish (Cardinale and Arrhenius 2000; Marteinsdottir and Begg 2002; Berkeley *et al.* 2004a; Berkeley *et al.* 2004b; Bokko and Berkeley 2004). However, no specific information on ABFT is yet available. Fromentin and Fonteneau (2001) hypothesized that the small spatial and temporal window available for

ABFT to reproduce (compared to tropical tunas) could increase temporal variability and, thus, result in higher risks of recruitment failure. But such an hypothesis presumes the existence of isolated population and would not be pertinent to the case of metapopulations. Santiago (1998) suggested that the North Atlantic Oscillation (NAO) might affect ABFT recruitment success, but further investigations tend to dismiss such hypothesis (Fromentin 2002c; ICCAT 2002b; Ravier and Fromentin 2003). Thus, the identification of the major abiotic and biotic forces controlling ABFT recruitment remains elusive, primarily due to limited direct observation.

In summary the ABFT spawning strategy and subsequently the recruitment success is likely to be more complicated than the usually postulated homing behaviour to small and permanent reproductive areas of the Western Mediterranean and Gulf of Mexico. The degree of complexity of the ABFT population structure on the one hand and the potential impact of environmental changes on the spatial and temporal distribution of the spawning areas on the other (Ravier and Fromentin 2004) are likely to shape and modify the reproductive strategy of ABFT in both in time and space.

Feeding

Like many marine fish, ABFT larvae appear to feed primarily on small zooplankton, mainly copepods and copepoda nauplii (Uotani *et al.* 1990). Whereas, juvenile and adult ABFT are opportunistic feeders (as are most predators). Chase (2002) counted at least 21 species of teleost fish, 2 of elasmobranch fish and at least 9 of invertebrates in the stomach samples of 568 ABFT and noted large differences among study areas, as well. The ABFT diet can include jellyfish and salps, as well as demersal and sessile species such as, octopus, crabs and sponges (Chase 2002 Ortiz-Zarate, pers. comm.). But in general, juveniles feed on crustaceans, fish and cephalopods, while adults primarily feed on fish such as herring, anchovy, sand lance, sardine, sprat, bluefish and mackerel (Ortiz de Zarate and Cort 1986; Eggleston and Bochenek 1990; Chase 2002). Typically, ABFT stomach contents are dominated by one or two prey-species, such as Atlantic herring and sand lance in the West Atlantic (Chase 2002) or anchovy in the East Atlantic and Mediterranean (Ortiz de Zarate and Cort 1986). No clear relationship has been demonstrated between prey length and the size of ABFT: both small and large ABFT display similar prey-size spectra. However, Chase (2002) noted that the largest prey (those greater than 40cm) were only consumed by giant ABFT greater than 230 cm. Usually it is postulated that adults do not feed during the spawning season, but this supposition remains poorly documented and disagrees with observations made by one of us (JMF during aerial surveys) and reported by fishermen.

Growth

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 attain a length of about 30-40 cm long and a weight of about 1 kg by October. After one year, fish reach about 4 kg and 60 cm long (Mather *et al.* 1995). Growth in length tends to be lower for adults than juveniles, but growth in weight increases. Therefore, juveniles are relatively slim, whereas adults are thicker and larger. At 10 years old, an ABFT is about 200 cm and 150 kg and reaches about 300 cm and 400 kg at 20 years (of course there is considerable variability between individuals). Maximum sizes (and probably age) appear to be much larger, as fish from 625 kg to 685 kg have been reported in Italian trap catches (Sara 1969) and an individual of 427 cm and 726 kg has been caught in the Gulf of Maine (Bigelow and Shroeder (1953). Purportedly, West ABFT grow faster after maturity and attain larger sizes than the East and Mediterranean ABFT (ICCAT 1997). A few studies also suggest that males grow faster than females and are proportionally more frequent in catches of individuals larger than

250 cm (Mather *et al.* 1995). Seasonal growth patterns have been better documented. Seasonal patterns have also been noted for the southern bluefin tuna, (Evenson2004). Both juvenile and adult ABFT grow rapidly during summer and early autumn (up to 10% per month), while growth is negligible in winter (Tiews 1957; Mather *et al.* 1995; Labelle *et al.* 1997). Additionally, Fromentin (Fromentin 2003) described significant year-to-year and decadal variations in weight-at-age of juveniles in the Western Mediterranean Sea, which could be related to environmental changes and/or age or size selection patterns of fishing.

Figure 4, about here

The ageing procedure used for ABFT has variously been based on the count of marks on hard structures, length-frequency data or mark-recapture data. Still, age-size relationships remain uncertain, especially for older individuals greater than 8 years. The count of annuli on otoliths, spines, vertebrae and scales are impaired by various sources of errors due to such factors such as the coalescence or the disappearance of the first marks or conversely to the multiple marking due to migration patterns (Compean-Jimenez and Bard 1980; Farrugio 1981; Compean-Jimenez and Bard 1983; Cort 1991; Mather *et al.* 1995). Decomposition of ABFT length-frequency data into age-classes (e.g., Bhattacharya 1967) becomes difficult for fish older than 5 years, as the cohorts tend to become indistinguishable. Also, intensive fishing on juveniles tends to smooth over modal differences that might have originally existed. Mark-recapture based growth curves used for ageing do not perform well for fish greater than 200 cm (~10 years old), either. 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 (Figure 4). The age estimate for a fish of 1 m and 2 m in length ranges over 3 and 6 years, respectively. 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 (error resulting from sample size, count of marks on hard structures, etc.) and process error (resulting from natural spatial and temporal variation in growth). 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 ABFT.

Fromentin and Fonteneau (2001) showed a clear contrast between life history traits of tropical tuna and ABFT. The former are 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 ABFT typically display opposite characteristics similar to cold-water species: slower growth, later maturity, shorter spawning season, larger size and longer life span. These life history traits make ABFT more vulnerable to exploitation than tropical tuna (Longhurst 1998; Fromentin and Fonteneau 2001).

Natural mortality

Like many fish populations, natural mortality rates of ABFT (denoted by the instantaneous annual rate, M) are poorly known. However, it is generally agreed that: (i) long-lived fish, such as ABFT, 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 (for a review on M, see e.g., Vetter 1987). Since ABFT 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 (Myers and Cadigan 1993; Fromentin *et al.* 2001). Predation purportedly comes mainly from large pelagic sharks and killer whales. Historical observations (as noted in the archives of the Dukedom of Medinia Sidonia) and recent studies (Nortarbartolo di Sciara 1987) indicate the occurrence of killer whales at the entrance of the Gibraltar Straits during the ABFT spawning migration. Also, it appears that the proportion of males is higher in catch samples of large individuals, which might indicate a higher M or lower growth for females ABFT (ICCAT 1997). However, differences in the sex ratio do not appear as strong as those for billfish or swordfish (Arocha and Lee 1996). 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) These rates are also relatively low in comparison to tropical tuna (ICCAT 1997; Hampton 2000). In the absence of direct and consistent estimates of M for ABFT, the natural mortality vector of the Southern bluefin tuna is generally used for the East-Atlantic and Mediterranean ABFT stock assessment, whereas a constant M of 0.14 is assumed for the West Atlantic ABFT (ICCAT 1999). However, both solutions remain unsatisfactory and tagging experiments and modelling are needed to progress on this issue (see “Perspectives” section).

Fisheries History

From Ancient Times to the 19th Century

Figure 5, about here

Archaeological excavations have shown that fishing on ABFT 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 2000). Ancient Greek or Roman poets and philosophers, such Aristotle, Pliny the Elder, Oppien and Aelien, gave extensive descriptions of fisheries exploiting ABFT migrating into the Mediterranean for spawning (see also Farrugio 1981; Mather *et al.* 1995; Doumenge 1998). At that time, fishermen primarily used hand lines and several varieties of seines, particularly beach seines. Between the 16th and 19th centuries, beach seines were progressively replaced by traps (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 (Figure 5) and substantial capital investment from Italian (mostly Genovese) bankers (Pavesi 1889; Berthelot 1988; Doumenge 2000).

The European scientific program STROMBOLI collated historical information from national and private archives, scientific libraries and various Mediterranean laboratories, then reconstructed and analysed more than one hundred time series of bluefin tuna trap catches since the 16th century (Fromentin 2002b). The mean range of the annual trap yields was estimated to have been about 15,000 tonnes per year, but with large fluctuations. Annual yields did not, however, seem to exceed 30,000 tonnes and were rarely below 7,000 tonnes, (Ravier and Fromentin 2002). These estimates confirmed the intensity of exploitation of ABFT by the ancient trap fisheries cited previously by historians.

Figure 6, about here

A striking result was the finding of a dominant 100-120 years periodic fluctuation in the trap catches (figure 6, 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), the authors postulated that this pseudo-cycle reflected variations in the abundance of ABFT 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 ABFT spawners in response to modifications in oceanographic conditions.

The 20th Century

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, ABFT 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 ABFT and North Atlantic albacore (*Thunnus alalunga*), arose in the Bay of Biscay during the mid-19th century (this fishery, which is nowadays mainly composed by bait boats, is still in activity, see Bard 1981). ABFT was also occasionally caught in the North Sea, Norwegian Sea and Kattegat since the 1930s by a new active gear, the purse seine (Meyer-Waarden 1959). These Nordic fleets grew rapidly such that their production exceeded that of the traditional trap fisheries during the 1950s, catching up to 16,000 tonnes/year (figures 2 and 7). Their catches were mainly composed of large ABFT 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 was the most important of the Nordic fleets (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, see “Ecology and Population Structure” section).

Figure 7, about here

During the same period, 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 8). Rod and reel sportfishing catches of juveniles were also important in some years. At that time purse seining of juveniles was the dominate portion of the catch. 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 (Figure 8). The longliners focused primarily on medium-sized fish, but concentrations of large fish were exploited if encountered (such the

Brazilian episode between 1962 to 1967 mentioned in ‘Migration and Stock delimitation’ section, Figures 2 and 7). During the 1970s, these fisheries moved to the Gulf of Mexico (the only known spawning area of the western Atlantic) to target large fish (Figure 8).

Figure 8, about here

The late 1960s and early 1970s were a transitory period for both the Atlantic and Mediterranean ABFT fisheries. The landings were lower than in the previous decades (~12,000 tonnes/year, Figure 7), 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 early 1970s in the West Atlantic (attributable to recruitment declines). Also during that period, purse seine and long-line fleets progressively replaced the traditional fisheries of the Mediterranean and East Atlantic.

The development of the Japanese sushi-sashimi market during the 1980s was the most remarkable event of recent decades, as it made ABFT 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. For instance, a standard French purse seiner in 1998 was twice as long and four times more powerful than it was in 1970 (engines were 170W and >800 W in 1970 and 1998, respectively) and further included powerful positioning and searching equipment, such as bird radars, sounders, sonars and planes (Liorzou 2001). Furthermore, new storage technologies (such as carrier vessels with deep freezing storage) and caging systems (for holding and fattening fish) were recently introduced and greatly modified both fishing strategies and efficiency (for a recent detailed report on the ABFT caging system, see Bregazzi 2004). 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 8). 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. Most recently the fisheries have expanded over the Central and Eastern basins such that ABFT is now exploited over the whole Mediterranean Sea (including offshore areas) 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 (Figure 8) was equally as striking. The redistribution of the fisheries resulted in rapid increases in yields since the 1980s, especially in the Mediterranean Sea. The Mediterranean has now regained its dominance as the most important fishing ground (Figure 7). 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. Catches are likely to have remained at around 40,000 to 50,000 tonnes for a decade (Fromentin 2003; ICCAT 2005). During the same period, a strict catch quota at around 2,500 tonnes was implemented in the West Atlantic.

Stock Status and Management

Background

ABFT is managed under the auspices of the International Commission for the Conservation of Atlantic Tunas (ICCAT); a convention of signatory member nations where the stated goal is the maximum sustainable catch of tuna and tuna-like species (ICCAT

2003a). Member nations annually provide catch and effort statistics from their tuna fisheries to the Secretariat of ICCAT, as well as results of relevant biological and ecological research. These data form the basis for developing scientific advice. Stock assessment analyses are performed by ICCAT's Standing Committee on Research and Statistics (SCRS) composed of national scientists from the member states. The Commission, itself, uses the scientific advice in negotiating binding agreements between member nations (the implementation is left to the authority of the member countries, for more details see http://www.iccat.es).

ICCAT and the SCRS have been concerned with the status of ABFT since the Commission's inception in the early 1970s (the first ICCAT recommendation was made in 1974 to limit effort and size limit on ABFT). However, comprehensive stock assessments of the resource began to be used in the late 1970s through the introduction of cohort analysis and virtual population analysis, i.e. untuned VPAs. Cohort analyses as they were constructed at that time required that catch, catch-at-age and natural mortality rates were known for the entire life-span of a cohort and that the population was closed. In the case of ABFT (as other species), each of the basic assumptions of the analytical methods have been questioned. Subsequently, auxiliary data (primarily catch-per-unit-effort (CPUE) indices of abundance) began to be included in the analyses in order to estimate trends of abundance in the most recent years of the analysis The approach used to compare VPA-derived abundance trends with CPUE's has gradually become more rigorous, progressing from maximization of correlation to least squares minimization and to, more recently, with the maximum likelihood estimation.

With the advent of more integrated methods of estimating status which utilized auxiliary information through tuning of ADAPT VPAs, the debate shifted to the CPUE's (i.e. the appropriateness of their use as indices of abundance or to the weighting of disparate indices representing different portions of the population) and to the magnitude of error in the catch and catch-at-age (which are assumed theoretically to be null, see e.g., Cotter *et al.* 2004). However, in many cases sampling has been sparse, especially in the 1960s and even in more recent years in the Mediterranean (see below). More statistically based models (Fournier *et al.* 1998) in which error structures of catch-at-age and other inputs are explicitly modelled, have been also explored (Porch and Turner 1997). While these methods have exposed some inconsistencies in the signals from catch-at-age data, tagging data and the CPUEs, no clear-cut solution to weighting these data presently exists for either these methods or more traditional ADAPT-VPAs.

However, the longest debate has centred on population structure and stock identification. In 1971, a one-stock hypothesis was deemed more plausible for the Atlantic with some separation between Atlantic and the Mediterranean components of the populations. In 1976, the SCRS considered factors which supported a two stock hypothesis (two stocks being the western Atlantic *versus* the eastern Atlantic and Mediterranean combined) and those supporting one-stock. The factors supporting two stocks included the occurrence of small to large fish on both sides of the ocean, the occurrence of spawning on both sides, no evidence of spawning activities in the mid-Atlantic, tagging and historical records of traps in the Gibraltar area that show ABFT entering into the Mediterranean spawning area, the distribution of larvae and juveniles in the Mediterranean and irregularities of trans-Atlantic tag returns (for a recent review, see ICCAT 2002a). On the other hand, factors supporting a one-stock hypothesis were similarity in growth rates and the occurrence of transatlantic tag returns. In 1980, the SCRS presented stock assessments separately for east and west stocks, and for a total Atlantic stock. The area divisions were suggested for statistical convenience and because they were aligned with discontinuities in the distribution of catches *at that time* in the Atlantic. The division line (i.e. 45^o W) adopted at the 1980 SCRS session was used to define the East and West stock management units. In 1981, the Commission set a “scientific monitoring level" for the West stock. Effectively, the scientific monitoring level was simply a TAC that was negotiated within the Commission. The goal was to set the level low enough to initiate recovery. The Commission continued to refer to this level as a scientific monitoring quota for some years, whereas the scientists simply referred to it as a TAC.

However, recent events in the fishery, coupled with new scientific evidence suggest that the simple East-West management boundary may no longer be the most appropriate mechanism for management. Electronic tagging indeed demonstrated that substantial movement of large ABFT from West to East occurred, but that the migration routes were complex (Block *et al.* 2001; Lutcavage *et al.* 2001). It was also showed that even small rates of net movement across the East-West boundary could have significant implications on assessment and projections (i.e., on future catch levels, Punt and Butterworth 1995). Just as significantly, ABFT fisheries moved and expanded. Originally, they tended to be located relatively close to the continents, but the central Atlantic region has become an important fishing ground since the 1990s (Figure 8). Consequently, the overall distribution of catch appears more continuous across the North Atlantic than was seen in previous decades (ICCAT 2002a). In response to the changing circumstances, research was conducted on alternative assessment methods which incorporate movement (e.g., Punt and Butterworth 1995; Turner and Powers 1995; Cooke and Lankester 1996; Porch and Turner 1999). In particular movement and mixing models focused on diffusion (where the probability of trans-Atlantic migration depends only on the location of the potential migrant) and overlap (where the ranges of the eastern and western populations are assumed merely to overlap). While understanding the characteristics of ABFT mixing through the development of a "true" model of movement is important, perhaps, a more important goal is to develop movement models that are useful for management purposes. For instance, Powers and Cramer (1996) suggested that incorporating reproductive behaviour of the stock into models is important, if the objective is to maintain a viable western spawning population, whereas it is less so if the objective is to maintain high yield ocean-wide. In response to this assessment research, the SCRS has begun to focus on appropriate management models, rather than defining a “correct” movement model or a single stock identification hypothesis (ICCAT 2002a).

Current Status

Currently, stock assessments continue to be conducted using VPA’s separately for the western Atlantic *versus* the eastern Atlantic plus Mediterranean (ICCAT 2003b). While the weaknesses associated with these assessments are known (see above), the analyses still provide a basis for management, because: i) consistent techniques are needed to monitor the recovery plan for the West component, ii) simulation studies suggested that more biases may be introduced into the assessment if mixing is inappropriately incorporated into the assessment models, iii) the much larger magnitude of abundance of the East Atlantic and Mediterranean ABFT compared to this of the West Atlantic ABFT meant that the dynamics of the West component had little influence on the East one (whereas, the converse is not true); (iv) the basic data deficiencies in the Mediterranean Sea made it difficult to reliably model the two components simultaneously. Nevertheless, ABFT assessments still explore mixing scenarios as sensitivity analyses.

Figure 9, about here

Catches of the West component 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 7). Additionally, the estimated spawning stock size (SSB) and recruits have been relatively stable since the mid-1980s (most of the declines occurring during the 1970s, Figure 9). However, the potential productivity of the stock, future recruitment levels, and the consequences of future catches on SSB trends remain uncertain and still lead to intensive debates.

Additionally, there are great uncertainties about the total catches and their size composition for many fisheries of the East Atlantic and Mediterranean ABFT since the late 1990s (ICCAT 2005). This together with the unknown adequacy of available CPUE indices as measures of overall stock abundance, make it difficult to interpret trends in SSB and recruits estimated from the VPA (Figure 9). For instance, the apparent regime shift in the recruitment during the early 1980s is likely to reflect the important changes in the selectivity pattern of the purse seiners. These fleets used to primarily catch juveniles ABFT, but they now target large fish during the spawning season in response to demand of the sushi-sashimi market. Consequently, the catch-at-size matrix of the East Atlantic and Mediterranean ABFT includes a much higher proportion of catches of large fish since the mid-1980s. In the absence of corresponding auxiliary information, the VPA naturally translates this change into a higher recruitment level since the early 1980s. However, it is unlikely that this higher level did, indeed, occur. Because of this uncertainty, the stock recruitment relationship was not an integral part of formulating the management advice. The productivity of the East stock has been estimated through different methods at around 25,000 tonnes (ICCAT 1997;1999;2003b). Despite potential biases due to various model assumptions and data quality, the recent estimates of productivity done by the SCRS are consistent with past studies (see e.g., Farrugio 1981).

Current Management

International conservation groups became more interested in the status of ABFT as the abundance of the resource declined particularly for the western component. Indeed, there was some impetus for the listing of ABFT under the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) in the early 1990's. This did not come to pass. However, the debate raised the issue of monitoring of the trade in ABFT. In response, ICCAT developed a "statistical document", i.e. a regulatory mechanism to require documentation of the trade of ABFT as it travels to the market primarily in Japan. The statistical document reduced the amount of unreported catches. Additionally, data derived from the documents provided scientists with a mechanism to make initial estimates of the unreported catches (ICCAT 2003c).

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 component should be at 2,500 tonnes (+/- 200 tonnes depending on future SCRS advice). For the East Atlantic and Mediterranean ABFT, the Commission recommended in 2002 that ABFT catches should not exceed 32,000 tonnes for the period 2002-2006 (since its implementation in 1998, the TAC varied between 29,500 and 32,000 tonnes).

Additionally, an Atlantic-wide size limit of 6.4 kg (i.e. age 2) has been in force since 1975. This was recently 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 ABFT (see above) and, as well as to differences in the fisheries. The West fisheries include an important recreational fishery (partly on juveniles) which has adapted to catch and release programs. Furthermore, commercial fishing in the West Atlantic mostly target large fish, whereas traditional fisheries in the East Atlantic and Mediterranean Sea still target small juveniles fish (see above). Size limits regulations in the East and Mediterranean may be more accepted by fishermen nowadays than they were in the past, as recent observers on board programs tend to show (Fromentin and Farrugio 2005). However, the situation probably varies among fleets and areas. Substantial amounts of under-size fish are still suspected to be caught in the East Atlantic and Mediterranean Sea because traditional and artisanal fisheries still target juveniles ABFT. However, the numerous landing locations make comprehensive control difficult. During the 1990s, the prohibition of longliners, purse seiners and aerial spotting planes have has been imposed in the Mediterranean Sea during given periods of the year (ICCAT 2004).

Figure 10, about here

In the East Atlantic and Mediterranean ABFT, these management regulations are believed not to have been very effective in limiting catches, especially in the Mediterranean Sea where significant misreporting has been suspected (figure 9, see also Fromentin and Ravier 2005; ICCAT 2005). The implementation of the TAC has induces incentives which cause perverse results for data collection (Fromentin 2003). The TAC regulation implies that the same information, i.e. the landings, is used to: (i) evaluate the state of the stock, (ii) manage and control the whole fishing activity and (iii) allocate quotas between contracting parties. The procedure, thus, describes a circle where the components of the system are tightly linked to one another. In an environment of overcapacity and high economical interests, it is difficult to completely avoid misreporting and fraud and, thus, the assessment-management system may be caught in a vicious circle. This is especially true when the stock is shared by many entities having divergent interests. Note that inefficiencies of TAC systems have also been questioned for some groundfish stocks (Cotter *et al.* 2004). Nevertheless, TAC systems can be and have been successful, especially when management regulations are adequately enforced and associated with appropriate incentives (Hilborn *et al.* 2004).

During a review of the fisheries data available for the East Atlantic and Mediterranean ABFT, ICCAT (2005) identified problems other than potential under-reporting: i) the presence of many data sets which are unclassified as to gear or are aggregated over gears, areas and seasons and ii) the lack of size composition of the catches for several major purse seine fleets (that represent more than 50% of the total Mediterranean yields). This problem has been mostly due to the development of caging and farming operations where fish are held in cages and fed and are not immediately landed. Thus, captured fish and the data associated with their size at capture were not normally accessible to scientists. The proportion of the catches which have been sampled for sizes and reported to ICCAT always fluctuated, but it dropped below 5% in the Mediterranean Sea since 1998. Consequently, many substitutions (data pooling strategies) have to be used to reconstruct the final catch-at-size and catch-at-age matrices. The SCRS, thus, concluded that it was no longer defensible to assess the East Atlantic and Mediterranean population using methods that assume that the catch-at-size (age) is known exactly, until extensive improvements in fisheries statistics are made. In the interim the efficacy of ‘more robust’ methods involving simple management procedures should be explored (ICCAT 2005). Note that the harmful effects of tuna farming on catch statistics, fishing pressure on small pelagic fish and introduction of viral diseases was also stressed by conservation organisations for several years (e.g. WWF 2002; WWF 2005).

For the West, there is a concern that the level of mixing across management unit boundaries might adversely affect the recovery in the West Atlantic. Essentially, increases in biomass of western fish may be moving across the border and being captured by eastern fisheries before they fully contribute to western recovery (ICCAT 2002a; Porch 2005). This concern has increased together with the growing intensity of exploitation in the East Atlantic and Mediterranean Sea and the accumulation of evidences of trans-Atlantic migrations from electronic tagging. Therefore, ICCAT (2002a) suggested several management and modelling approaches to address these spatial problems. Most promising is the development of operating models, i.e. models integrating biological realism with robust management procedures (Powers and Porch 2004, Kell *et al.* 2003). These approaches allow contrasting and competitive biological and ecological hypotheses to be tested for their utility and robustness against various management scenarios. These could greatly help assessment and management of various kinds of situations, including data poor situations (2002a; Powers and Porch 2004).

Perspectives

Status and futures of the stocks

Large uncertainties in the basic fisheries statistics for the East Atlantic and Mediterranean ABFT together with the lack of knowledge on key processes in the population dynamics (reproduction, migration and population structure) have strongly influenced and, possibly, biased the perception of the status of both the East and West stocks. For instance, the evaluations done in the 1970s and early 1980s underestimated ABFT productivity. Thus, it might be tempting to argue that these large uncertainties allow for postponement of the implementation and control of more ambitious management measures, justifying the *status-quo*. Nevertheless, despite the current uncertainties, we believe that ABFT as a whole has been undergoing heavy overfishing for a decade. Indeed, the intensity of the current exploitation is the highest of the long history of ABFT fisheries in the Mediterranean Sea (Fromentin 2003; ICCAT 2003c). The current capacity of the purse seine fleet (more than 200 units in the Mediterranean Sea) and longline fleet together exceed the mean productivity of ABFT (estimated at ~25,000 tonnes and 2,500 tonnes for East and the West stock, respectively, ICCAT 1999; ICCAT 2003b). Furthermore, the historical perspective given by the centuries-old trap fisheries and the Nordic fisheries indicates that current yields in the East Atlantic and Mediterranean Sea are more than two times higher than historical records and mean estimated productivity as well (see above). Lastly, the spatial expansion of the fisheries has considerably reduced the area where ABFT is *not* exploited; this is a spatial expansion that is directly related to the sharp increase of the fishing pressure and fishing efficiencies during the two last decades rather than to a change in ABFT spatial distribution.

ABFT fisheries in the Mediterranean provide an illustration of a rendition of the 'race-for-fish' strategy described by Hilborn *et al.* (2003). Normally, the race-for-fish is conducted by competing fishers to get the most fish prior to the TAC be reached. In this case the race is to capture as much market and infrastructure as possible before the TAC is meaningfully implemented. It remains unclear to what extent improvements in TAC implementation for the East Atlantic and Mediterranean ABFT has slowed this process. This situation, coupled with the life history characteristics of ABFT, very high value and relatively poor monitoring suggest that the exploitation of ABFT has many biological and economic traits that have led several fish stocks to depletion in the past (Hilborn *et al.* 2003). The challenge is now as much (and maybe more) organizational and institutional as it is scientific. While from a scientific viewpoint the priority is to obtain adequate and reliable fisheries statistics, the future of ABFT might also involve important modifications to access and governance structures (Hilborn *et al.* 2005).

Research priorities

Improvements in scientific research are necessary but not sufficient conditions for improvements in long-term management. However, better understanding of key ecological processes is also needed, especially on the habitat and the spatial dynamics of this highly migratory species. The success with which we take up this challenge will depend on our ability to collect novel fishery-independent observations. Such a novel method to do this is through the use of archival tags and their associated "bio-loggers". While there is no doubt that bio-logging technologies have produced impressive results during the last decade (see e.g., Gunn and Block 2001), their technical development and scientific utilization still has considerable limitations: 1) electronic tags have been developed for use with different species and for different research goals and are built and commercialised in small numbers.

Consequently, they often remain too expensive for large-scale experiments (~4,000 € per pop-up archival tag); 2) geolocation in archival tags is deduced from light information and is, thus, impaired by relatively large errors of about 1 to 3 degrees in average (i.e. 60 to 180 nautical miles); this magnitude of error is inconsequential for broad-based location studies, but the same magnitude of error becomes excessive when correlating movements with fine-scale oceanographic events (Sibert *et al.* 2003; Teo *et al.* 2004; Royer *et al.* 2005); 3) tag attachment needs to be improved to avoid numerous premature jettisons, 4) satellite transmission of pop-up tags can fail for various reasons such as lack of satellite coverage in the area of the pop-up and bad weather conditions; 5) current archival pop-up tags can still only be implemented on large fish; 6) the resulting data have not been fully exploited, as the ecological or oceanographic context is not easily accessible to biologists. Therefore, technical improvements are still needed to create effective, reliable, widely-usable bio-logging devices, as well as to integrate a framework to acquire, process, store, and visualize tag data coupled with the ocean descriptions now operationally available from remote sensing and numerical ocean models.

As we believe that the spatial dynamics of ABFT is central to understanding the population dynamics of this species, electronic tagging is expected to be an important tool. Nonetheless, electronic studies alone will not be sufficient to get a comprehensive picture of ABFT population dynamics. It is also critical to discriminate between putative spawning sites and nurseries of tagged fish to get a better understanding of the population structure. To do so, there is firstly a need to better understanding the spatial and temporal dynamics of reproduction of ABFT (see above). Trans-Atlantic surveys (using the same sampling protocol throughout the Atlantic and Mediterranean) of both adults and larvae would, thus, be necessary. Furthermore, genetic analyses and micro-chemistry have been recently applied to ABFT to test for the presence of discrete populations between regions of the Mediterranean

Sea and North Atlantic. Therefore to build upon these initial successes, it is important to develop protocols and logistic feasibility plans for applying these techniques on large samples encompassing the entire spatial distribution of ABFT. Additionally, these techniques need to be improved so that they can be routinely used to determine the geographical and genetic origins of older individuals, i.e. the spawners.

Genetic tagging is a technique that has recently emerged as a mechanism to estimate population parameters. This technique that might have potential for application to ABFT uses genetic markers (DNA) as individual tags. This has two great advantages in comparison to conventional tagging: it avoids most of the post-release mortality and it allows one to obtain an unbiased estimate of reporting rates (see e.g., Palsbøll *et al.* 1997; Taberlet *et al.* 1999). Thus, genetic tagging might constitute an interesting and powerful alternative approach to estimate mortality rates and population sizes of ABFT. It would provide valuable information to investigate the ABFT population structure, as well. But this technique may require rather extensive (and costly) sampling for both release and recapture. However, the potential for genetic tagging is so promising for ABFT that its feasibility should be explored in near future.

Modeling of ABFT needs to expand beyond the traditional stock assessment approaches. The renewed importance of spatial dynamics and population structure means that these factors must be directly dealt with in both the modeling and in the management structure. “Operating models” need to be developed which depict biological, ecological and fisheries “reality” in some detail, exploring a range of hypotheses, e.g. how the population is really structured, how fish move, the sparseness of catch data and other factors. Then management procedures could be developed and tested against the operating models with the goal of deriving management techniques which are robust to data deficiencies and where risks and tradeoffs are explored transparently. For instance, if evidences from genetic analyses, micro-chemistry or genetic tagging tend to support a meta-population structure (see above), then operating models could be designed, so that ABFT would be divided in several corresponding management units (indeed in that case, the traditional two stocks hypothesis would not make sense anymore).

Regardless of the modeling and management mechanisms chosen, there is a need for better monitoring of juvenile abundance and better understanding recruitment dynamics of ABFT. The lag in information imposed by having to wait until fish mature before abundance signals become clear means that managers have little flexibility to adjust to stock dynamics. Previously, the feasibility for aerial surveys as a mechanism for monitoring juveniles has been done (Lutcavage *et al.* 1997; Fromentin *et al.* 2003). More integrated approaches using airplanes, vessels and electronic tagging may make monitoring more efficient. Experimental designs and initial pilot surveys should be developed leading to juvenile relative abundance monitoring programs.

Finally, it would be worthwhile to initiate a data prospecting and data recovery effort for the catch composition of the fisheries operating during the 1950s, 1960s and 1970s in the North Atlantic and Mediterranean Sea. The analysis of these data is likely to provide valuable and original insights into ABFT spatial dynamics, as these three decades were marked by remarkable variations in the spatial distributions (possibly abundances) of ABFT in the North Atlantic.

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References

Addis, P., Cau, A., Davini, M.A., Secci, E. and Scibaldi, G. (1997) Collection of tuna data catches by trap-nets in Sardinia: historical (1825-1980) and recent catches (1992-1995). *Collective Volume of Scientific Papers ICCAT* **46,** 132-139.

Aristote (IV B.C.) *Histoire des animaux. Chapitre 13. Les migrations des poissons.* Gallimard - folio essais, Paris.

Arocha, F. and Lee, D.W. (1996) Maturity at size, reproductive seasonality, spawning frequency, fecundity and sex ratio in swordfish from the Northwest Atlantic. *Collective Volume of Scientific Papers ICCAT* **45,** 350-357.

Bard, F.X. (1981) *Le thon germon Thunnus alalunga (Bonaterre 1788) de l'océan atlantique.* Thèse de Doctorat d'Etat. Université Pierre et Marie Curie, Paris 6, 330 pp.

Bard, F.X. (2001) Extension of the geographical and vertical habitat of albacore (*T. alalunga*) in the North Atlantic. Possible consequences on true rate of exploitation of this stock. *Collective Volume of Scientific Papers ICCAT* **52,** 1447-1456.

Bard, F.X., Bach, P. and Josse, E. (1998) Habitat et écophysiologie des thons : Quoi de neuf depuis 15 ans? *Collective Volume of Scientific Papers ICCAT* **50,** 319-342.

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

Berkeley, S.A., Hixon, M.A., Larson, R.J. and Love, M.S. (2004b) Fisheries Sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* **29,** 23-32.

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

Bhattacharya, C.G. (1967) A simple method of resolution of a distribution into Gaussian components. *Biometrics* **23,** 115-135.

Bigelow, H.B. and Schroeder, W.C. (1953) Fishes in the Gulf of Maine. *Fisheries Bulletin and Wildlife Service* **53,** 1-577.

Block, B.A., Dewar, H., Blackwell, S.B. *et al.* (2001) Migratory Movements, Depth Preferences, and Thermal Biology of Atlantic Bluefin Tuna. *Science* **293,** 1310-1314.

Block, B.A., Teo, S.L.H., Walli, A. *et al.* (2005) Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* **434,** 11211127.

Bokko, S.J. and Berkeley, S.A. (2004) Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*). *Fishery Bulletin* **102,** 418-429.

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

Bregazzi, R.M. (2004) Tuna Ranching Intelligent Unit - September 2004*. Advanced Tuna Ranching Technologies (ATRT),* Madrid**,** 49 pp.

Brill, R.W. and Lutcavage, M.E. (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., Lutcavage, M.E., Metzger, G. *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.

Broughton, R. and Gold, R.J. (1997) Microsatellite development and survey of variation in northern bluefin tuna (*Thunnus thynnus*). *Molecular Marine Biology and Biotechnology* **6,** 308-314.

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

Carey, F.G. and Robinson, B.H. (1981) Daily patterns in the the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fisheries Bulletin* **79,** 277-292.

Carlsson, J., McDowell, J.R., Diaz-Jaimes, P. *et al.* (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. In: *World meeting on stock assessment of bluefin tunas: strengths and weaknesses* (eds R.B. Deriso and W.H. Bayliff), IATTC, La Jolla, pp. 181-350.

Cetti (1777) *Storia naturale della Sardegna.* Piattoli, Sassari.

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.

Clark, J. (1968) Seasonal movements of striped bass contingents of Long Island Sound and New York Bight. *Transactions of the American Fisheries Society* **97,** 320-343.

Compean-Jimenez, G. and Bard, F.X. (1980) Age and growth of East Atlantic bluefin tuna as determined by reading of fin rays cross section. *Collective Volume of Scientific Papers ICCAT* **9,** 547-552.

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

Cooke, J.G. and Lankester, K. (1996) Examination of alternative stock distribution models for the interpretation of bluefin tuna (*thunnus thynnus*) tag-recovery data. *Collective Volume of Scientific Papers ICCAT* **45,** 135-138.

Cort, J.L. (1991) Age and growth of the bluefin tuna *Thunnus thynnus* (L.) of the Northeast Atlantic. *Collective Volume of Scientific Papers ICCAT* **35,** 213-230.

Cotter, A.J.R., Burt, L., Paxton, C.G.M., Fernandez, C., Buckland, S.T. and Pan, J.-X. (2004) Are stock assessment methods too complicated? *Fish and Fisheries* **5,** 235-254.

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. *Ministerio de Marina-Direccion General de Pesca*, Madrid**,** 1-118.

de Metrio, G., Arnold, G.P., Block, B.A. *et al.* (2002) Behaviour of post-spawning Atlantic bluefin tuna tagged with pop-up satellite tags in the Mediterranean and eastern Atlantic. *Collective Volume of Scientific Papers ICCAT* **54,** 415-424.

Desse, J. and Desse-Berset, N. (1994) Stratégies de pêche au 8$^{\text{ème}}$ millénaire : les poissons de Cap Andreas Kastros (Chypre). In: *Fouilles récentes à Khirokitia* (eds A. Le Brun), Editions Recherche sur Civilisations, Paris, pp. 335-360.

Dittman, A.H. and Quinn, T.P. (1996) Homing in Pacific salmon: mechanisms and ecological basis. *Journal of Experimental Biology* **199,** 83-91.

Dodson, J.J. (1988) The nature and role of learning on the orientation and migratory bahaviour of fishes. *Environmental Biology of Fishes* **23,** 161-182.

Doumenge, F. (1998) L'histoire des pêches thonières. *Collective Volume of Scientific Papers ICCAT* **50,** 753-803.

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

Eggleston, D.B. and Bochenek, E.A. (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., Stoner, D.S., Dean, J.M. *et al.* (2002) Genetic analyses of Atlantic northern bluefin tuna captured in the northwest Atlantic Ocean and the Mediterranean Sea. *Collective Volume of Scientific Papers ICCAT* **54,** 372-376.

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

Farley, J.H. and Davis, T.L.O. (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. Université des Sciences et Techniques du Languedoc, 266 pp.

Fournier, D.A., Hampton, J. and Sibert, J.R. (1998) MULTIFAN-CL: a length-based, age-structured model fo fisheries stock assessment, with application to south Pacific albacore, *Thunnus alalunga*. *Canadian Journal of Fisheries and Aquatic Science* **55,** 2105-2116.

Fromentin, J.-M. (2002a) Descriptive analysis of the ICCAT bluefin tuna tagging database. *Collective Volume of Scientific Papers ICCAT* **54,** 353-362.

Fromentin, J.-M. (2002b) Final report of STROMBOLI - EU-DG XIV project 99/022. *European Community - DG XIV*, Brussels**,** 109 pp.

Fromentin, J.-M. (2002c) Is the recruitment a key biological process in the hypothetical NAO-Atlantic tunas relationships? *Collective Volume of Scientific Papers ICCAT* **54,** 1008-1016.

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 Farrugio, H. (2005) Results of the 2003 observer program on board of the French purse seiner targeting Atlantic bluefin tuna in the Mediterranean sea. *Collective Volume of Scientific Papers ICCAT* **57,** in press.

Fromentin, J.-M., Farrugio, H., Deflorio, M. and de Metrio, G. (2003) Preliminary results of aerial surveys of bluefin tuna in the western Mediterranean Sea. *Collective Volume of Scientific Papers ICCAT* **55,** 1019-1027.

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

Fromentin, J.-M., Myers, R.M., Bjørnstad, O., Stenseth, N.C., Gjøsæter, J. and Christie, H. (2001) Effects of density-dependent and stochastic processes on the stabilization of cod populations. *Ecology* **82,** 567-579.

Fromentin, J.-M. and Ravier, C. (2004) 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* **in press**.

Fromentin, J.-M. and Ravier, C. (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.

Graham, J.B. and Dickson, K.A. (2001) Anatomical and physiological specializations for endothermy. In: *Tuna. Physiology, ecology, and evolution* (eds B.A. Block and E.D. Stevens), Academic Press, San Diego, pp. 121-165.

Gunn, J. and Block, B.A. (2001) Advances in acoustic, archival, and satellite tagging of tunas. In: *Tuna. Physiology, ecology, and evolution* (eds B.A. Block and E.D. Stevens), Academic Press, San Diego, pp. 167-224.

Hampton, J. (2000) Natural mortality rates in tropical tunas: size really does matter. *Canadian Journal of Fisheries and Aquatic Science* **57,** 1002-1010.

Hamre, J., Lozano, F., Rodriguez-Roda, J. and Tiews, K. (1968) Report from the bluefin tuna working group. *Conseil Permanent international pour l'Exploration de la Mer*, Copenhagen**, Statistical News letters No 38,** 27p.

Hanski, I. (1999) *Metapopulation Ecology.* Oxford University Press, Oxford.

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.

Hilborn, R., Branch, T.A., Ernst, B. *et al.* (2003) States of the world fisheries. *Ann. Rev. Environ. Resour.* **28,** 15.1-15.40.

Hilborn, R., Orensanz, J. and Parma, A. (2005) Institutions, incentives and the future of fisheries. *Phil. Trans. R. Soc. B* **360,** 47-57.

Hilborn, R., Punt, A.E. and Orensanz, J. (2004) Beyond band-aids in fisheries management: fixing world fisheries. *Bull. Mar. Sci.* **74,** 493-507.

Holland, K.N., Brill, R.W., Chang, R.K.C., Sibert, J.R. and Fournier, D.A. (1992) Physiological and behavioural thermoregulation in bigeye tuna (*thunnus obesus*). *Nature* **358,** 410-412.

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

ICCAT (1997) 1996 SCRS detailed report on bluefin tuna. *Collective Volume of Scientific Papers ICCAT* **46,** 1-301.

ICCAT (1999) 1998 SCRS detailed report on bluefin tuna. *Collective Volume of Scientific Papers ICCAT* **49,** 1-191.

ICCAT (2002a) ICCAT workshop on bluefin tuna mixing. *Collective Volume of Scientific Papers ICCAT* **54,** 261-352.

ICCAT (2002b) Report of the ICCAT Workshop on environment and tuna recruitment (Madrid, Spain, May 7-12, 2001). *Collective Volume of Scientific Papers ICCAT* **54,** 895-952.

ICCAT (2003a) Basic Texts. *International Commission for the Conservation of Atlantic Tuna (ICCAT),* Madrid**, 3rd revision,** 113 pp.

ICCAT (2003b) Report of the 2002 Atlantic Bluefin Tuna Stock Assessment Session. *Collective Volume of Scientific Papers ICCAT* **55,** 710-937.

ICCAT (2003c) Report of the Sixth GFCM-ICCAT Meeting on Stocks of Large Pelagic Fishes in the Mediterranean. *Collective Volume of Scientific Papers ICCAT* **55,** 1-84.

ICCAT (2004) 14th Report of the Standing Committee on Research & Statistics (SCRS). *International Commission for the Conservation of Atlantic Tuna (ICCAT),* Madrid**,** 206 pp.

ICCAT (2005) Report of the 2004 data exploratory meeting for the East Atlantic and Mediterranean bluefin tuna. *Collective Volume of Scientific Papers ICCAT* **57,** in press.

Inagake, D., Yamada, H., Segawa, K., Okazaki, M., Nitta, A. and Itoh, T. (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., Oray, I., Corriero, A. *et al.* (2004) First information on the reproductive biology of the bluefin tuna (Thunnus thynnus) in the eastern Mediterranean. *Collective Volume of Scientific Papers ICCAT* **56,** 1158-1162.

Kritzer, J.P. and Sale, P.F. (2004) Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries* **5,** 131-140.

Labelle, M., Hoch, T., Liorzou, B. and Bigot, J.L. (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., Fiedler, P.C. and Montgomery, D.R. (1984) Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep Sea Research* **31,** 1085-1099.

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

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of Entomological Society of America* **15,** 237-240.

Lioka, C., Kani, K. and Nhhala, H. (2000) Present status and prospects of technical developmment of tuna sea-farming. *Cahiers Options Méditerranéennes* **47,** 275-285.

Liorzou, B. (2001) Final report of the EU project BFTMED (97/029). *European Community - DG XIV,* Brussels**,** 325 pp.

Longhurst, A. (1998) Cod: perhaps if we all stood back a bit? *Fisheries Research* **38,** 101-108.

Lutcavage, M., Brill, R.W., Skomal, G.B., Chase, B.C. and Howey, P.W. (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., Kraus, S. and Hoggard, W. (1997) Aerial survey of giant bluefin tuna, *Thunnus thynnus*, in the great Bahama bank, straits of Florida, 1995. *Fish. Bull.* **95,** 300-310.

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. *Collective Volume of Scientific Papers ICCAT* **52,** 759-770.

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

MacCall, A.D. (1990) *Dynamic geography of marine fish populations.* Washington Sea Grant, Seattle.

Marsac, F. (1999) Changements hydroclimatiques observés dans l'Atlantique depuis les années 50 et impacts sur quelques stocks de thons et leur exploitation. *Collective Volume of Scientific Papers ICCAT* **49,** 346-370.

Marteinsdottir, G. and Begg, G.A. (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., Mason Jr, J.M. and Jones, A. (1995) Historical document: life history and fisheries of Atlantic bluefin tuna. *NOAA Technical Memorandum NMFS-SEFSC-370,* Miami**,** 165 pp.

McQuinn, I.H. (1997) Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries* **7,** 297-329.

Medina, A., Abascal, F.J., Megina, C. and García, A. (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., Brill, R.W., Boggs, C.H., Curran, D.S., Kazama, T.K. and Seki, M.P. (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.

Myers, R.A. and Cadigan, N.G. (1993) Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Science* **50,** 1576-1590.

Nishikawa, Y., Honma, M., Ueyanagi, S. and Kikawa, S. (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.

Olivieri, I., Couvet, D. and Gouyon, P.-H. (1990) The genetics of transient populations: Research at the metapopulation level. *Trends in Ecology & Evolution* **5,** 207-210.

Ortiz de Zarate, V. and Cort, J.L. (1986) Stomach contents study of immature bluefin tuna in the Bay of Biscay. *ICES-CM* **H:26,** 10 pp.

Palsbøll, P.J., Allen, J., Bérubé, M. *et al.* (1997) Genetic tagging of humpbackwhales. *Nature* **388,** 767-769.

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

Picinetti, C. and Piccinetti Manfrin, G. (1993) Distribution des larves de thonidés en Mediterranée. *Collective Volume of Scientific Papers ICCAT* **40,** 164-172.

Pline, l.a. (Ith A.C.) *Histoire Naturelle. Livre IX.* Les Belles Lettres, Paris.

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. and Turner, S.C. (1997) Catch-at-age analysis of West Atlantic bluefin tuna incorporating data from 1960 to 1994. *Collective Volume of Scientific Papers ICCAT* **46,** 276-279.

Porch, C.E. and Turner, S.C. (1999) Virtual population analyses of Atlantic bluefin tuna with alternative models of transatlantic migration. *Collective Volume of Scientific Papers ICCAT* **49,** 291-305.

Porch, C.E., Turner, S.C. and Powers, J.E. (2001) Virtual population analyses of Atlantic bluefin tuna with alternative models of transatlantic migration: 1970-1997. *Collective Volume of Scientific Papers ICCAT* **52,** 1022-1045.

Powers, J.E. and Cramer, J. (1996) An exploration of the nature of Atlantic bluefin tuna mixing. *Collective Volume of Scientific Papers ICCAT* **45,** 173-181.

Powers, J.E. and Porch, C.E. (2004) Approaches to developing management procedures which incorporate mixing. *Collective Volume of Scientific Papers ICCAT* **56,** 1144-1152.

Pujolar, J.M. and Pla, C. (2000) Genetic differentiation between north-west Atlantic and Mediterranean samples of bluefin tuna (*Thunnus thynnus*) using isozyme analysis. *Collective Volume of Scientific Papers ICCAT* **51,** 882 - 891.

Punt, A.E. and Butterworth, D.S. (1995) Use of tagging data within a VPA formalism to estimate migration rates of bluefin tuna accross the North Atlantic. *Collective Volume of Scientific Papers ICCAT* **44,** 166-182.

Pusineri, C., Ravier, C. and Fromentin, J.-M. (2002) Retrospective analysis of the bluefin tuna Nordic fisheries data. *Collective Volume of Scientific Papers ICCAT* **54,** 517-526.

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

Ravier, C. and Fromentin, J.-M. (2002) Eastern Atlantic bluefin tuna: what we learnt from historical time-series of trap catches. *Collective Volume of Scientific Papers ICCAT* **54,** 507-516.

Ravier, C. and Fromentin, J.-M. (2003) Long-term fluctuations in bluefin tuna trap catches: Are they environmentally driven? *Collective Volume of Scientific Papers ICCAT* **55,** 1208-1216.

Ravier, C. and Fromentin, J.-M. (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.

Roffer, M.A. (1987) *Influence of the environment on the apparent abundance of juvenile Atlantic bluefin tuna along the United States east coast.* Ph.D dissertation. University of Miami, 154 pp.

Rooker, J.R. and Secor, D.H. (2004) Stock structure and mixing of Atlantic bluefin tuna: Evidence from stable δ13C and δ18O isotopes in otoltihs. *Collective Volume of Scientific Papers ICCAT* **56,** 1115-1120.

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

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

Royer, F., Fromentin, J.-M. and Gaspar, P. (2005) A state/space model to derive bluefin tuna movement and habitat from archival tags. *Oikos* **109,** 473-484.

Santiago, J. (1998) The North Atlantic Oscillation an recruitment of temperate tunas. *Collective Volume of Scientific Papers ICCAT* **48,** 240-249.

Sara, R. (1963) Data, observations and comments on the occurence, behavior, characteristics and migrations of tunas in the Mediterranean. *Procedings of the General Fisheries Council for the Mediterranean* **8,** 371-388.

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. In: *Tuna. Physiology, ecology, and evolution* (eds B.A. Block and E.D. Stevens), Academic Press, San Diego, pp. 225-270.

Schick, R.S., Goldstein, J. and Lutcavage, M.E. (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.

Scordia, C. (1938) Per la biologia del tonno (Thunnus thynnus L.) XV. Le migrazioni dei tonni entro il Mediterraneo. *Memorie di Biologia Marina di Oceanografia, Messina* **5,** 1-50.

Secor, D.H. (1999) Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fisheries Research* **43,** 13-34.

Secor, D.H., Campana, S.E., Zdanowicz, V.S., Lam, J.W.H., Yang, L. and Rooker, J.R. (2002) Inter-laboratory comparison of Atlantic and Mediterranean bluefin tuna otolith microconstituents. *ICES Journal of Marine Science* **59,** 1294-1304.

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. *R. Comitato Talassografico Italiano* **Memoria 156,** 511-542.

Sibert, J.R., Musyl, M.K. and Brill, R.W. (2003) Horizontal movements of bigeye tuna near Hawaii from archival tagging data. *Fisheries Oceanography* **12,** 141-151.

Sinclair, M. (1988) *Marine populations: an essay on population regulation and speciation.* Washington Press, Seattle.

Sinclair, M. and Iles, T.C. (1989) Population regulation and speciation in the oceans. *Journal du Conseil international pour l'Exploration de la Mer* **45,** 165-175.

Slatkin, M. and Wade, M.J. (1978) Group selection on a quantitative character. *Proceedings of the National Academy of Science US* **75,** 3531-3534.

Smith, P.J. and Jamieson, A. (1986) Stock discreteness in herrings: a conceptual revolution. *Fisheries Research* **4,** 223-234.

Susca, V., Corriero, A., Deflorio, M., Bridges, C.R. and De Metrio, G. (2001) New results on the reproductive biology of bluefin tuna (*Thunnus thynnus*) in the Mediterranean. *Collective Volume of Scientific Papers ICCAT* **52,** 745-751.

Taberlet, P., Waits, L.P. and Luickart, G. (1999) Non-invasive genetic sampling:look before you leap. *Trends in Ecology & Evolution* **14,** 323-327.

Teo, S.L.H., Boustany, A., Blackwell, S., Walli, A., Weng, K.C. and Block, B.A. (2004) Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. *Marine Ecology Progress Series* **283,** 81-98.

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. (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. and Powers, J.E. (1995) Review of information related to Atlantic bluefin tuna east-west movement. *Collective Volume of Scientific Papers ICCAT* **44,** 191-197.

Turner, S.C., Restrepo, V.R. and Eklund, A.M. (1991) A review of the growth rate of West Atlantic bluefin tuna, *Thunnus thynnus*. *Collective Volume of Scientific Papers ICCAT* **35,** 271-293.

Uotani, I., Saito, T., Hiranuma, K. and Nishikawa, Y. (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., El Tawil, M. and Pla, C. (2001) Preliminary genetic analyses of Mediterranean bluefin tuna caught in Libyan waters. *Collective Volume of Scientific Papers ICCAT* **52,** 797-802.

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

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

WWF (2002) Tuna farming in the Mediterranean: the 'coup de grâce' to a dwindling population? When bluefin tuna becomes golden tuna. *WWF publications*, WWF Mediterranean Programme Office**,** 14 pp.

WWF (2005) Risk on local fish populations and ecosystems posed by the use of imported feed fish by the tuna farming industry in the Mediterranean. *WWF publications*, WWF Mediterranean Programme Office**,** 11 pp.

Legends

Figure 1. Spatial distribution of Atlantic bluefin tuna (gray shading) and main migration routes (black arrows) are deduced from current and historical fisheries data as well as traditional and electronic tagging information (see text for references). The vertical dashed line depicts the stock delimitation between the two current ICCAT management units. The main spawning grounds (dark dotted gray areas) being currently assumed in the literature are located in the Mediterranean Sea and the Gulf of Mexico.

Figure 2. Catches of Atlantic bluefin tuna by the Nordic fisheries (i.e. Norway, Germany, Denmark and Sweden) between 1930 and 1990 (ICES and ICCAT data) and by the Japanese longline fisheries in the southwest Atlantic, offshore Brazil (ICCAT data).

Figure 3. Size composition of the catches of the Norwegian fleet targeting bluefin tuna in the North Sea (1964 to 1981 ICES reports of the bluefin tuna working group).

Figure 4. Corresponding curves of the 16 Von Bertalanffy equations published by various authors since Sella (1929) for the Atlantic buefin tuna (the 2 curves currently used by the SCRS for the East and West stock assessments are highlighted by thicker lines).

Figure 5. Picture of a traditional tuna fisheries during the 17th century close to Cadiz (South of Spain, from G. Braun and F. Hogenberg, 1612 - Civitates Orbis Terrarum, Colonia). In this area, migrating bluefin tuna through the Gibraltar straight were detected by guards standing at the top of the towers. Fish were caught by large beach seines and directly canned in local manufactories. Beach seines implied a greater amount of workforce than traps (the latter replacing the former in the western Mediterranean since the 16th century and along the Spanish coast during the early 19th century). Most of these fisheries constituted important

establishments with a real economic stack and bankers were often involved in trap management.

Figure 6. Plots of long time series (between 80 and 360 years long) of Atlantic bluefin tuna catches from 8 traps between 1599 and 1960 (catches are expressed in the log-number of fish caught over a given year, for more details see Ravier and Fromentin 2001; 2004). The 8 traps were set along the West coast of Sicily, North and South coasts of Sardinia, South coast of Portugal and North coast of Tunisia. A few traps are still set nowadays.

Figure 7. Official total catches of Atlantic bluefin tuna between 1950 and 2003 reported to ICES and ICCAT. Total catches are split in the three main geographical areas, i.e., the Mediterranean Sea, the East and West Atlantic. Catches mainly occurred in the northeast Atlantic (North Sea and Norwegian Sea) during the 1950s, in the West Atlantic during the mid-1960s (offshore northern Brazil) and in the Mediterranean since the 1970s.

Figure 8. Total catches of ABFT per decades (1960-1969; 1970-1979; 1980-1989 and 1990-1999), per geographical locations (5°x5° square) and per main gears: bars represent the total catches of surface gears (i.e., mostly purse seine, but also bait boat, hand line and trap); circles represent the total catches of long line.

Figure 9. Results of the retrospective analyses for the East Atlantic and Mediterranean stock (left panel) and West Atlantic stock (right panel) from the 2002 SCRS bluefin tuna stock assessment (ICCAT 2003b). Spawning stock biomass (top graphs) and recruitment (bottom graphs) are given for the base cases. Note the differences in scaling between both stock (estimates from the East stock being 5 to 10 times higher than these of the West).

Figure 9. Comparison of Task I nominal catches for the East Atlantic and Mediterranean bluefin tuna stock, as reported to ICCAT secretariat in 1996, 1998, 2000, and 2003. Differences between series mainly come from a major revision of the catch made by various fishing entities in 1998, i.e. after the implementation the TAC on the East stock. These revisions concern the 1990-1996 period and are likely to reflect over-reporting, as the quota of each entity is proportional to its historical catches. The relative differences between the 1996 and 2000 Task I series can exceed 20% in some years.

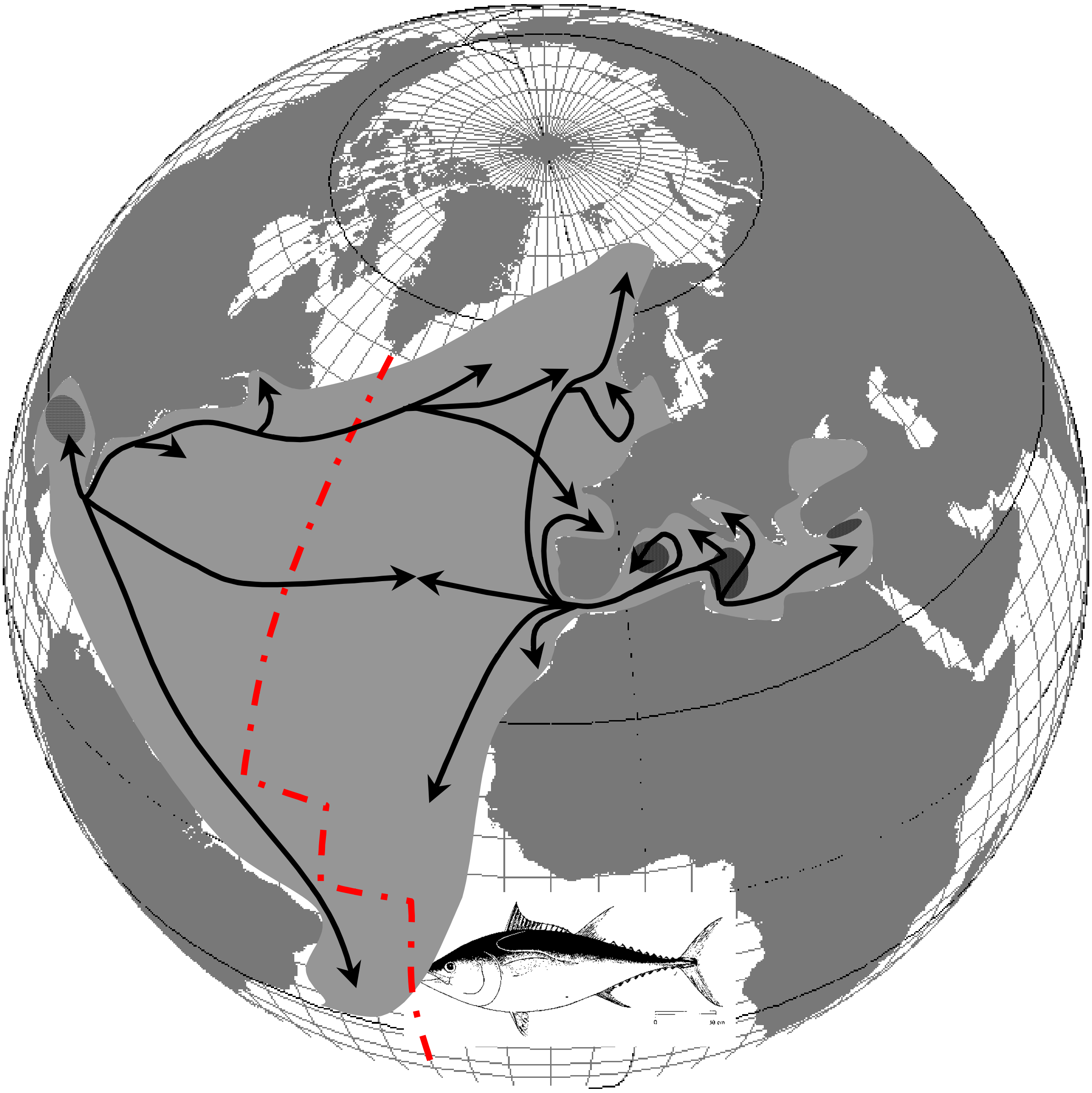
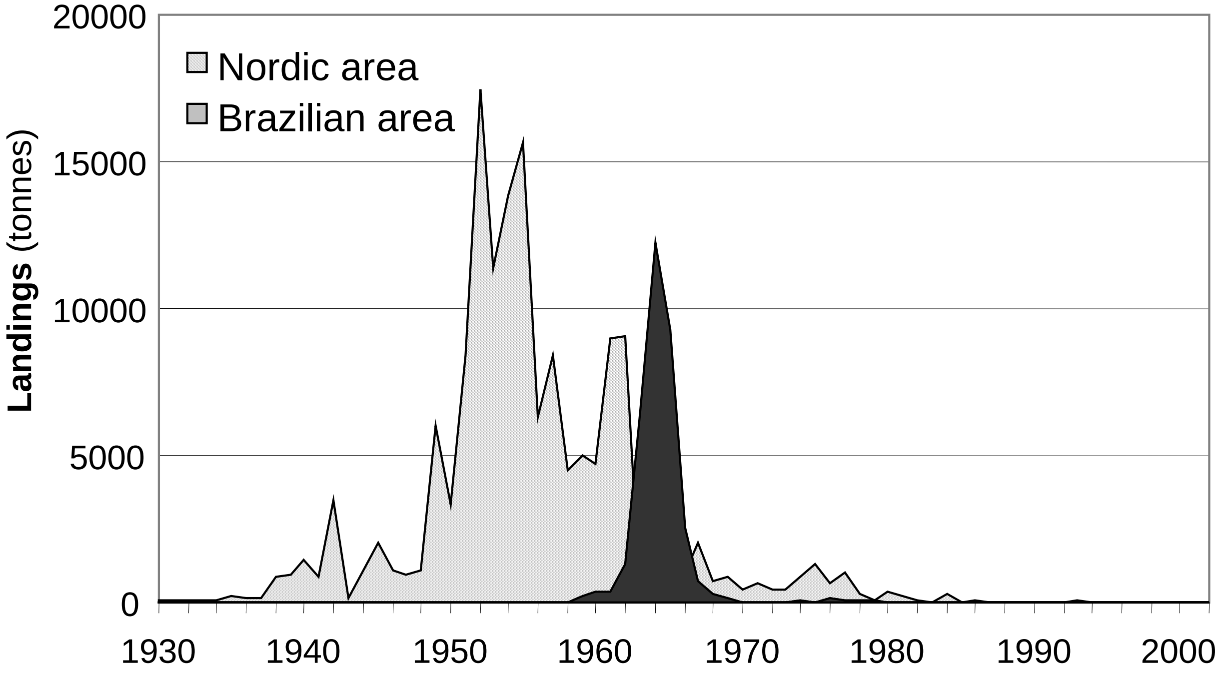


Figure 1



20000
15000
10000
5000
0
Landings (tonnes)
Nordic area
Brazilian area
1930
1940
1950
1960
1970
1980
1990
2000

Figure 2

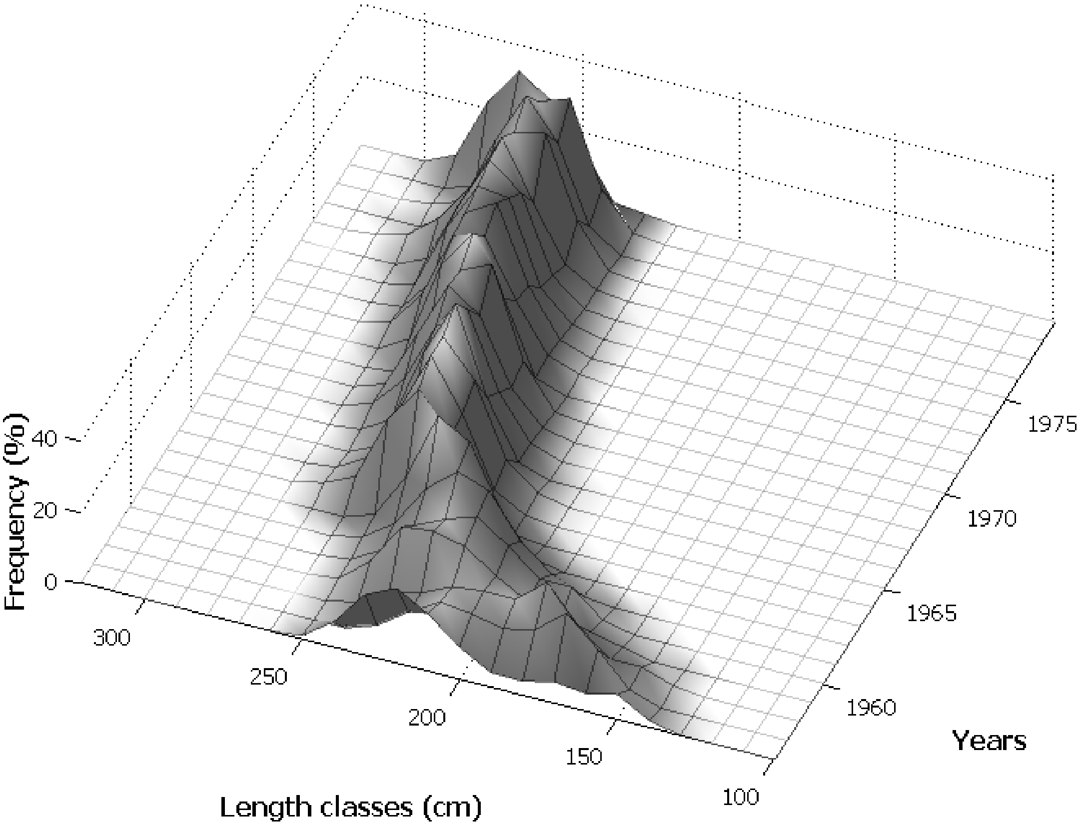

Frequency (%)
40
20
0
300
250
200
150
100
Length classes (cm)
1975
1970
1965
1960
Years

Figure 3

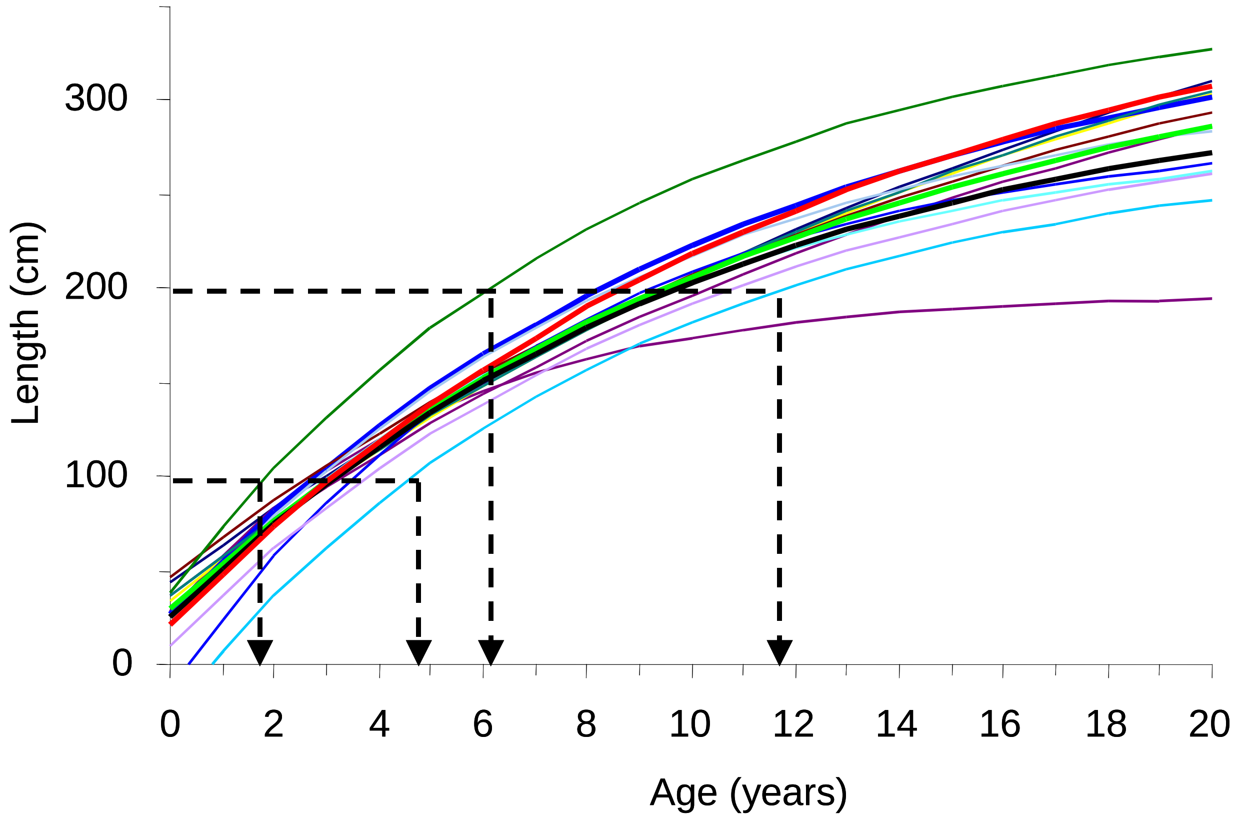


Figure 4


1. Mar Oceano.
2. Sant Sebastiano.
3. Santa Catherina.
4. Torres de Guardia.
5. Yglesia mayor.
Castillo. 6.
7. Puerta del muro.
8. Cannas para la yela.
9. Puntal.
10. Goertas de Safia.
11. Arenas.
12. Torres de Hercules.
13. Scanca.
14. La Baya.
15. Los puercos.
16. Tierra firma d Espanna.
17. Punta de Sant Lucar.
18. Sermona.
19. Rotta.
20. Sant Catalina.
21. Pa barra.
22. Puerto Sta Maria.
23. Mar Oceano.
24. La Ysola.
Effigiauit et communicauit Georgius Houfnaglius.
Almadraua de Calitz
SIVE THYNNORVM PISCATIO APVD GADES
15
19
16
14
12
17
18
9
24

Figure 5

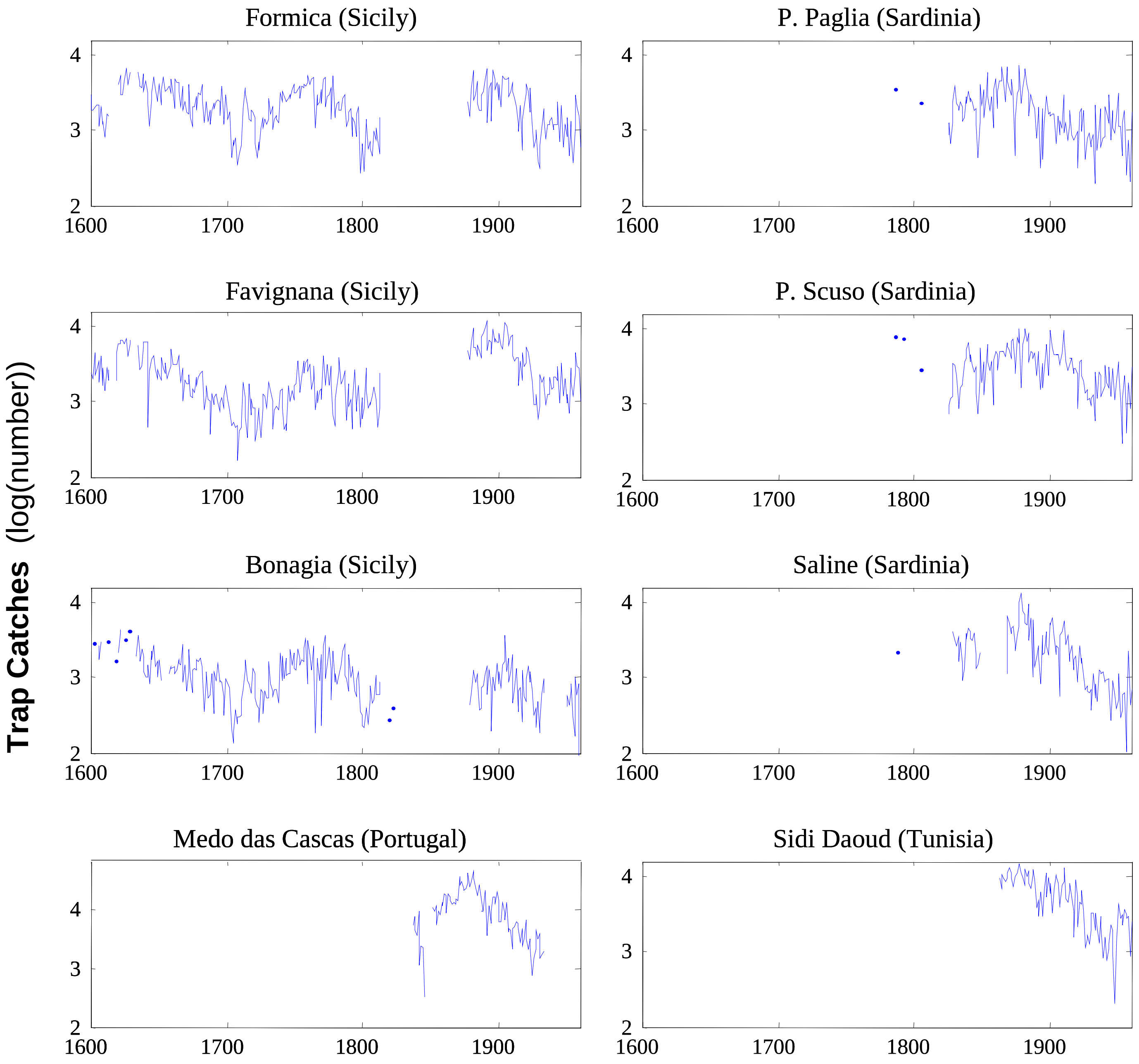

Trap Catches (log(number))
Formica (Sicily)
P. Paglia (Sardinia)
Favignana (Sicily)
P. Scuso (Sardinia)
Bonagia (Sicily)
Saline (Sardinia)
Medo das Cascas (Portugal)
Sidi Daoud (Tunisia)
2
3
4
1600
1700
1800
1900

Figure 6

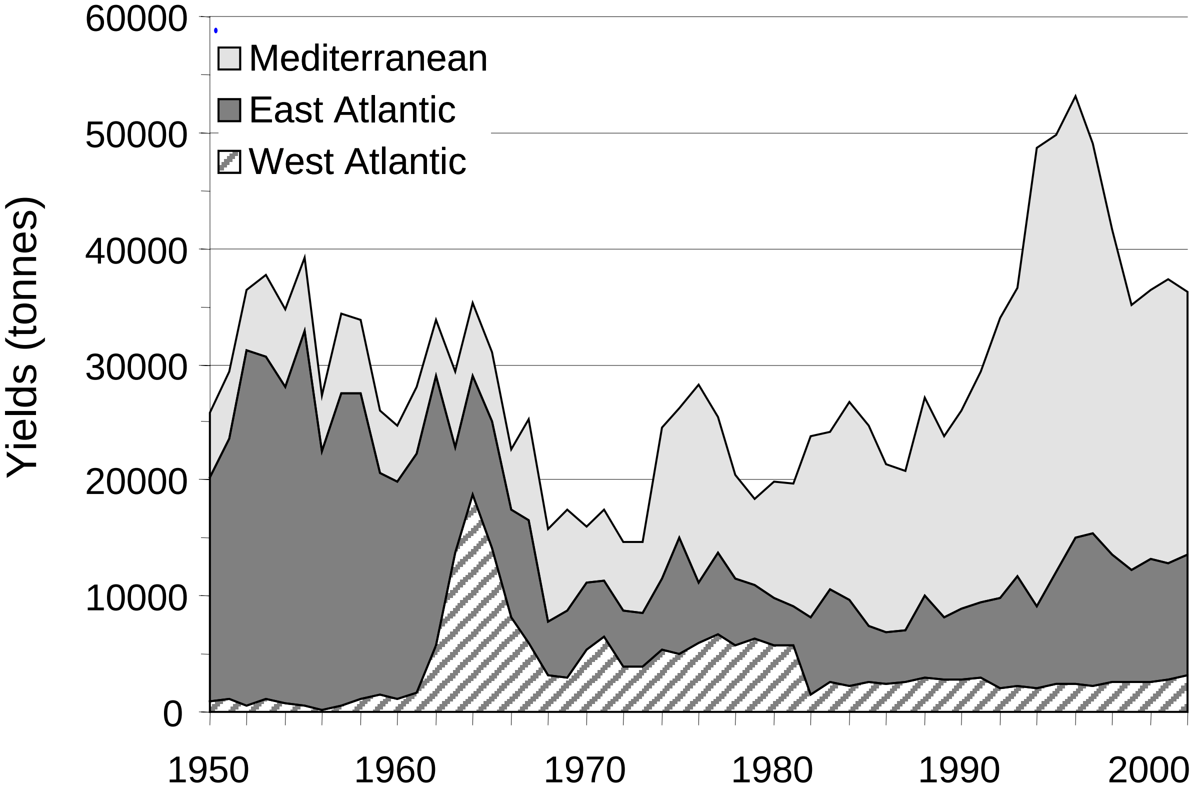

60000
50000
40000
30000
20000
10000
0
Yields (tonnes)
Mediterranean
East Atlantic
West Atlantic
1950
1960
1970
1980
1990
2000

Figure 7

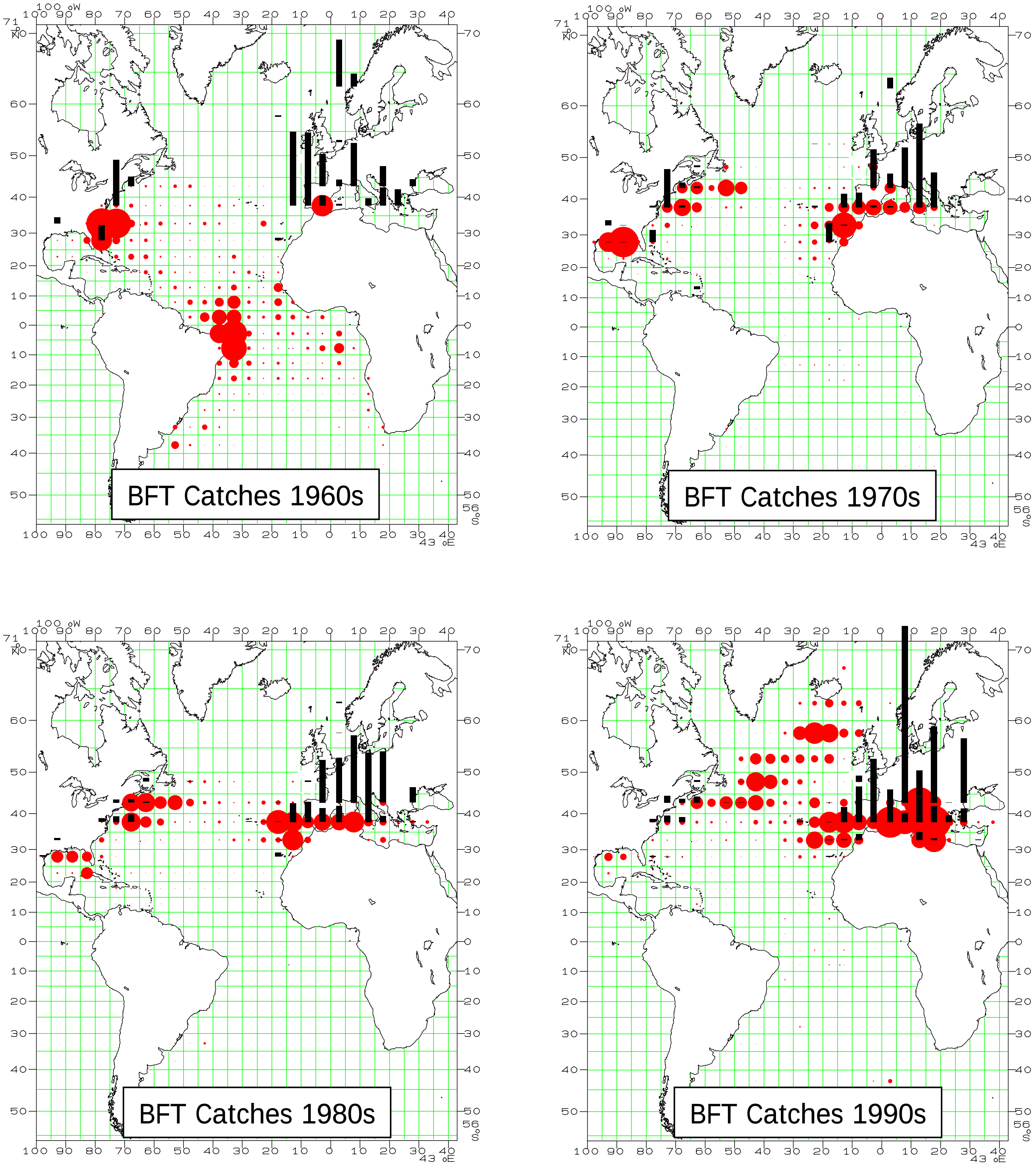

BFT Catches 1960s
BFT Catches 1970s
BFT Catches 1980s
BFT Catches 1990s
100 oW
71 oN
100 90 80 70 60 50 40 30 20 10 0 10 20 30 40
70 60 50 40 30 20 10 0 10 20 30 40 50
43 oE
56 oS

Figure 8

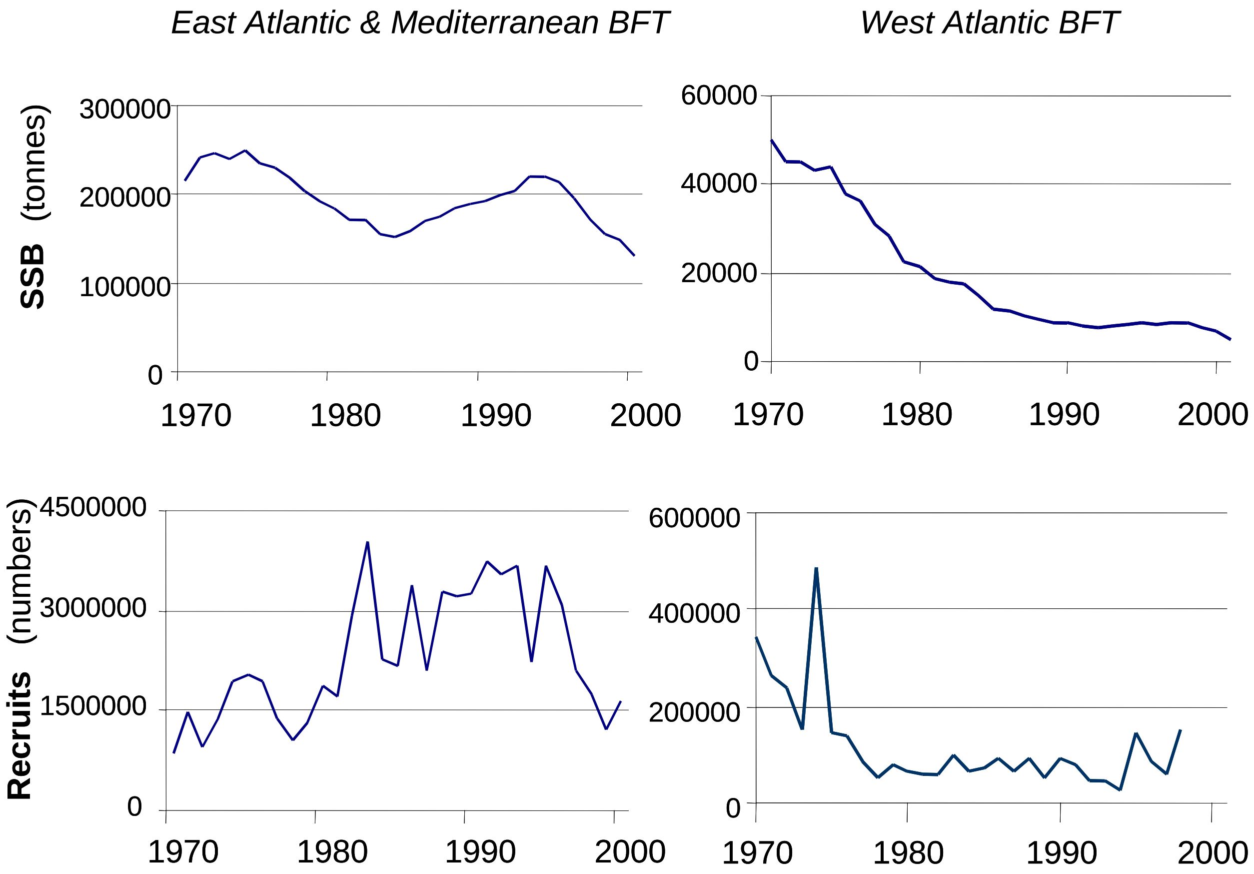

East Atlantic & Mediterranean BFT
West Atlantic BFT
SSB (tonnes)
300000
200000
100000
0
60000
40000
20000
0
1970
1980
1990
2000
Recruits (numbers)
4500000
3000000
1500000
0
600000
400000
200000
0
1970
1980
1990
2000

Figure 9

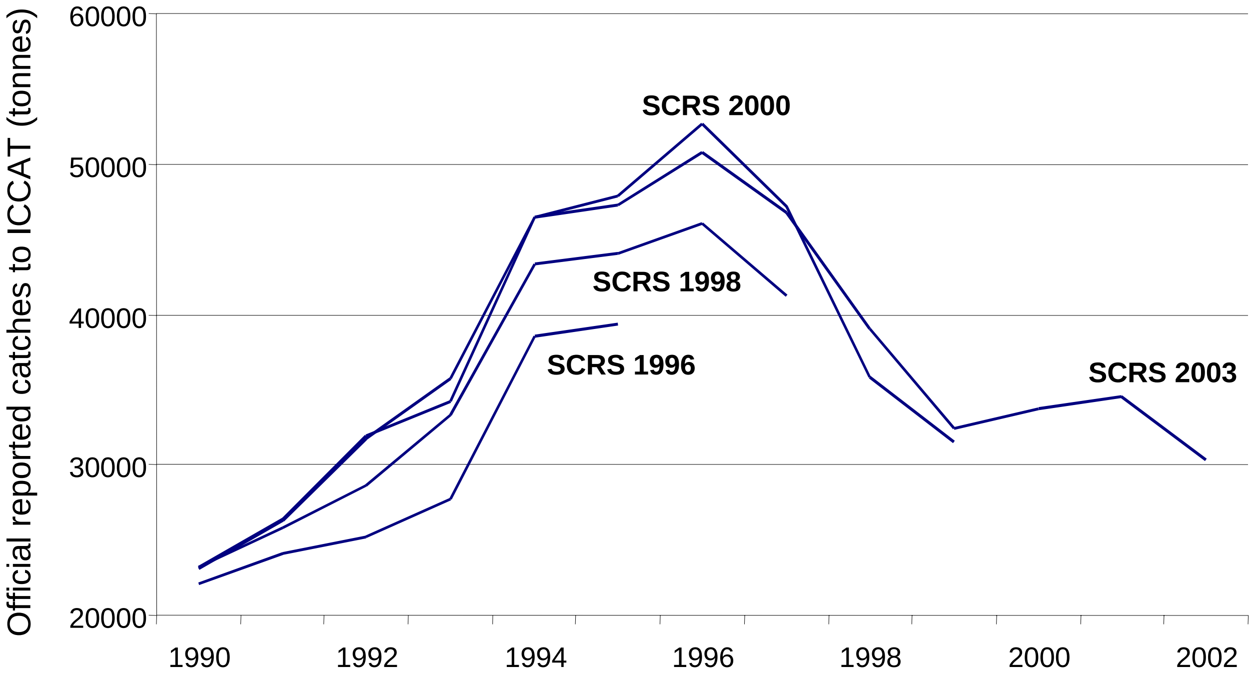

Official reported catches to ICCAT (tonnes)
60000
50000
40000
30000
20000
1990
1992
1994
1996
1998
2000
2002
SCRS 2000
SCRS 1998
SCRS 1996
SCRS 2003

Figure 10