Putting all the pieces together: integrating current knowledge of the biology, ecology, fisheries status, stock structure and management of yellowfin tuna (Thunnus albacares)

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Putting all the pieces together: integrating current knowledge of the biology, ecology, fisheries status, stock structure and management of yellowfin tuna (*Thunnus albacares*)

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Abstract Yellowfin tuna (*Thunnus albacares*; YFT) is an apex marine predator inhabiting tropical and subtropical pelagic waters. It supports the second largest tuna fishery in the world. Here, we review the available literature on YFT to provide a detailed overview of the current knowledge of its biology, ecology, fisheries status, stock structure and management, at global scale. YFT are characterized by several peculiar anatomical and physiological traits that allow them to survive in the oligotrophic waters of the pelagic realm. They are opportunistic feeders, which allows fast growth and high reproductive outputs. Globally, YFT fisheries have expanded over the last century, progressively moving from coastal areas into the majority of sub-tropical and tropical waters. This expansion has led to a rapid increase in global commercial landings, which are predominantly harvested by industrial longline and purse seine fleets. For management purposes, YFT is divided into four stocks, each of which is currently managed by a separate tuna Regional Fisheries Management Organization. Our current understanding of YFT stock structure is, however, still uncertain, with conflicting evidence arising from genetic and tagging studies. There is, moreover, little information about their complex life-history traits or the interactions of YFT populations with spatio-temporally variable oceanographic conditions currently considered in stock assessments. What information is available, is often conflicting at the global scale. Finally, we suggest

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future research directions to manage this valuable resource with more biological realism and more sustainable procedures.

Introduction

Tunas (Scombridae, Perciformes) are highly mobile pelagic ray-finned fishes with widespread distributions and a wide range of life-history attributes (Juan-Jordá et al. 2013a, b; Murua et al. in press). For centuries, tunas have been targeted by fisheries due to their high economic value and extensive international trade (Ravier and Fromentin 2001; Miyake et al. 2010). In 2014, landings of the main commercially fished tunas reached a record high, topping more than 5.5 million metric tons (MT). In the last decade, yellowfin tuna (*Thunnus albacares*; YFT) landings have averaged around 1.25 million MT per year, making it the second largest tuna fishery in the world. The management of YFT stocks comes under the jurisdiction of four tuna Regional Fisheries Management Organizations (tRFMOs): the Inter-American Tropical Tuna Commission (IATTC) in the Eastern Pacific Ocean (EPO), the Western-Central Pacific Fisheries Commission (WCPFC) in the Western and Central Pacific Ocean (WCPO), the International Commission for the Conservation of Atlantic Tunas (ICCAT) and the Indian Ocean Tuna Commission (IOTC) (Fromentin et al. in press). The primary goal of tRFMOs is to maintain the stocks of tuna and tuna-like species at levels which allow maximum sustainable yield (MSY). To achieve this overarching objective, management and conservation strategies typically implement regulations such as catch quotas, time-area closures and fishing capacity limits, many of which rely on annual or multi-annual stock assessments (Juan-Jordá et al. 2011; Aranda et al. 2012).

The global assessment of tuna stocks suggests that most are currently harvested at levels close to their MSYs, while longer-living, high value species such as bluefin tunas (*Thunnus thynnus* and *Thunnus orientalis*) have already been subject to overfishing (Collette et al. 2011; Juan-Jordá et al. 2011). However, some tuna species such as YFT and bigeye tuna (*Thunnus obesus;* BET) have also experienced overfishing in the Atlantic Ocean (AO) and Pacific Ocean (PO). The most recent YFT stock assessment carried out in 2015 for the Indian Ocean (IO) YFT concluded that the status of this stock was overfished and, that overfishing is currently occurring (IOTC 2015).

These stocks are however associated with high levels of uncertainty. Tuna stock assessments are mostly based on fishery-dependent data such as nominal catch, size frequency data, and abundance indices derived from commercial catch per unit effort (CPUE). Fishery-dependent data are known to be subject to several biases, primarily stemming from underreporting or misreporting of nominal catches, lack of spatial catch and effort data as well as size samples for many fisheries (Geehan and Pierre 2015). In the case of YFT, stock assessments heavily rely on abundance indices derived from Japanese longline fisheries which have been substantially decreasing over the last decade and spatially contracting, resulting in a major decrease in size samples, changes in CPUE representativeness as well as changes in targeting that are poorly understood. Also, technological changes in gears and attributes are poorly monitored despite the fact that they are known to have increased fishing efficiency over time (Maufroy et al. 2016; Tidd et al. 2016). In addition, the high mobility of industrial tuna fleets, as well as changes in the distribution of tuna species in relation to environmental conditions, have biased abundance indices derived from CPUE data (Walters 2003; Rouyer et al. 2010). Finally, while our current knowledge of tuna biology is crucial for estimating the reproductive potential of fish stocks and predicting recruitment dynamics (Marshall et al. 2006), research into this area has been neglected over the last few decades (Juan-Jordá et al. 2013a, b).

Using YFT as an example, we seek to illustrate the current mismatch between the economic importance of a species, which globally support major commercial and recreational fisheries, and the paucity of biological and ecological information available and employed in the management of its fishery. In addition, tuna stocks are currently assessed based on administrative boundaries, while information on biological stock structure and genetic integrity are considered to be of secondary importance (Carvalho and Hauser 1995; Ward 2000; Fromentin et al. in press). To begin, we review and synthesize the large amount of available biological

and ecological information on YFT. Using this information, we show how unique physiological and anatomical traits, coupled with vertical migratory behavior and an opportunistic feeding strategy, allow YFT to occupy very large expanses of the world's oceans. We then collate and compile catch data from the tRFMOs to reconstruct the history of YFT fisheries over almost a century and assess their current global scale distribution.

We also reviewed the data used in the current stock assessment models worldwide for critically describing and evaluating fundamental aspects of YFT populations, such as growth, reproduction, and stock structure and status, in order to provide a comprehensive overview of the current state of knowledge. We also include and update older regional-scale information obtained from previous reviews (Sund et al. 1981; Cayré et al. 1988; Wild 1994). We also note that our current understanding of YFT population structure is characterized by a high degree of uncertainty across different oceans and conflicting evidence in the literature (Ely et al. 2005; Pecoraro et al. 2016). Finally, we suggest future research directions to address the identified knowledge gaps so that we may begin to address current YFT stock assessment and management challenges.

From physiology to habitat utilisation

Anatomical and physiological features

YFT display anatomical and physiological features and adaptations that allow them to operate as apex predators in the epipelagic realm where prey are patchily distributed (Korsmeyer and Dewar 2001). For example, YFT possess several structural characteristics that enhance swimming performance (Magnuson 1979; Brill and Bushnell 1991; Brill 1996). YFT have a fusiform and elongate body shape that is deepest under the first dorsal fin and tapers towards the caudal peduncle. This body shape improves movement through the water and minimizes hydrodynamic lift (Fig. 1). The caudal peduncle also includes three sets of bony keels that reduce drag and possibly direct water over the middle part of the fin (Aleyev 1977). In large individuals, the second dorsal and anal fins are very long (>20% of the fork length; FL) and behind both those fins, seven to ten dorsal and ventral finlets
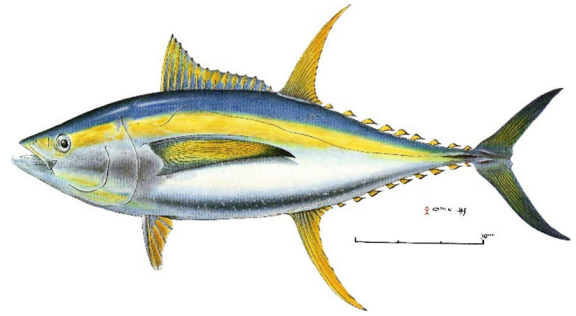
Fig. 1 Yellowfin tuna (*Thunnus albacares*). ©P Opic

are present. These finlets limit the cross flow of water between the two sides of the body, further reducing drag (Altringham and Block 1997). The pectoral fins are moderately long, usually reaching the base of the second dorsal fin, and are used to counteract negative buoyancy. The swim bladder is small, making the fish denser than seawater. It is only present in anterior half of body cavity and can be deflated or slightly inflated. Besides the sturdy, fusiform body shape, the anterior localization of the muscle mass and the insertion of myotomes over a greater number of vertebrae improve the ability of YFT to undertake high-performance swimming activities at sustained speeds (Westneat and Wainwright 2001). Like other tunas and lamnid sharks, YFT have myotomes with long cones (Bernal et al. 2001; Block et al. 1993). Red muscle tissue is located in an anteriomedial position and is completely surrounded by white muscle tissue (Graham and Dickson 2004). These anatomical char-acteristics reduce regional bending, thus lengthening the propulsive wavelengths and ensuring that the muscular force is focused on the semi-lunate caudal fin. This fin is predominantly responsible for the portion of the tail-beat cycle in which the tuna's main thrust is generated (Dewar and Graham 1994). Although YFT's tail-beat frequencies and amplitude range are similar to those of other scombrids, they produce considerably longer propulsive wavelengths and maximum stride length values (Dewar and Graham 1994). Further, this efficient swimming activity is never interrupted to ventilate the gills. The gills are structured to facilitate increased levels of oxygen (O_2) uptake, maintain hydrostatic equilibrium, deliver O_2 to sustain red muscle activity as well as to meet other highly aerobic metabolic demands (Magnuson 1979; Brill 1987). To meet the O_2 uptake and delivery needs associated with their high standard

metabolic rate, YFT also feature several cardiorespiratory adaptations, such as a large heart with a thick and compact myocardial layer, a large stroke volume and well-developed coronary circulation. They also have high hemoglobin and hematocrit concentrations, both of which are known to enhance O_2 carrying capacities (Korsmeyer et al. 1997; Graham and Dickson 2004). However, despite these adaptations, YFT are sensitive to reductions in ambient O_2 concentrations, a situation that occurs at elevated depths (Bushnell et al. 1990; Bushnell and Brill 1992). Nonetheless, YFT is more tolerant to hypoxia than skipjack tuna (*Katsuwonus pelamis;* SKJ) and other actinopterygian fishes (Davis 1975). YFT also have some thermal-dependent metabolic and physiological processes, such as heart function, digestion, gastric evacuation and assimilation, which may limit their distribution. To address these physiological constraints, the heat produced during metabolic activities is conserved due to the more axial positioning of the red muscle and the presence of both central and lateral counter-current heat exchangers (*retia mirabilia*). Although the lateral *retia* is relatively small, it prevents heat from being carried off by the blood and lost through the gills (Carey and Teal 1966; Brill 1987, 1996; Altringham and Block 1997; Graham and Dickson 2000).

The endothermic capacity of YFT has important implications for cardiac functions that control the heart rate and the delivery of O_2 to the red muscle tissues (Korsmeyer et al. 1997). Together with high myoglobin levels, elevated temperatures increase the rate of O_2 diffusion from the capillaries to the mitochondria, promoting aerobic metabolic activities (Stevens and Carey 1981). Thus, the big advantage of YFT's endothermic capabilities is the increased aerobic function of the red (Dickson 1996), and, possibly, white (Graham and Dickson 2000) muscle tissues. Conversely, under some circumstances, this capability can cause severe overheating problems, even at sustainable swimming speeds (Sharp and Vlymen 1978).

Feeding strategy

The evolution of YFT's morphological and physiological adaptations have allowed the species to travel over immense oceanic areas, searching for sporadic prey that give them the energy required to support their

continuous and high metabolic activities. In the open ocean, the relationship between local prey densities and foraging efficiency is essential for the survival and abundance of YFT. As with other tuna species, YFT are considered to be "energy speculators" due to their high rates of energy turnover in nutrient poor environments, such as the open ocean (Korsmeyer et al. 1997). YFT are opportunistic predators, feeding on a great variety of prey species, including crus-taceans, fish, cephalopods and gelatinous organisms (Potier et al. 2005). In the IO, YFT preferred prey include the nomeid *Cubiceps pauciradiatus* and the swimming crab *Charybdis smithii* (Potier et al. 2005, 2007; Zudaire et al. 2015). During the South-West and North-East monsoon seasons of 2002 2005, the endemic stomatopod *Natosquilla investigatoris* that formed huge pelagic swarms which invaded the entire western region (Romanov et al. 2015), becom-ing the main YFT prey item during these events (Potier et al. 2005, 2007). Despite their opportunistic behavior, the diet composition of YFT has been shown to be size-dependent (Ménard et al. 2006; Zudaire et al. 2015), with an ontogenetic feeding shift. Small individuals (<40 cm FL) mainly feed on euphasiids and planktonic preys, while larger individuals (>50 cm FL) mainly feed on fishes, crustaceans and cephalopods. This shift has been observed in Sri Lankan waters (Maldeniya 1996) and was further corroborated by stable isotope analyses of carbon ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) and nitrogen ($^{15}N/_{14}N$, expressed as $\delta^{15}N$) ratios. These ratios provide longer, time-integrated assessments of YFT dietary sources, as well as additional information on their trophic position, the origin of the carbon consumed and their migration and foraging strategies (Lorrain et al. 2015; Young et al. 2015; Sardenne et al. 2016).

In Hawaiian waters, stable isotope studies indicate that YFT's foraging niche width increases dramatically at 45 cm FL, in relation to a switch from coastal to open sea prey species (Graham et al. 2007). More recently, Sardenne et al. (2016) showed that for IO YFT, isotopic signatures of N and C in the liver changed with size, reflecting an increased ability to consume different prey. This was described by the wide range of observed $\delta^{15}N$ values. This shift may be driven by size associated increases in endothermic capability that allow individuals to dive more deeply and as a result, access a wider range of prey (Graham et al. 2007; Sardenne et al. 2016). Small sized YFT are

typically found in multi-species schools associated with drifting floating objects while most larger specimens occur in free-swimming schools (FSC; see "Yellowfin tuna fisheries" section).

Although YFT are considered to be day-feeders, displaying higher activity levels between sunrise and sunset (Reintjes and King 1953; Júnior et al. 2003), they have also been reported to feed at night (Olson and Boggs 1986). The mean daily ratio of ingested food is estimated to be between 2.8 and 4.5% of body weight. YFT are able to reach these levels after only 30 min of feeding (Olson and Boggs 1986). This ratio increases with size until individuals reach 60 70 cm FL, after which it declines (Maldeniya 1996). Thus, we deduce that YFT habitat utilization is strongly influenced by the presence of high prey density (Schaefer et al. 2007), as observed in the case of *Natosquilla investigatoris* in the IO (see above). This situation was observed in the northern areas of the EPO and WCPO where high prey densities were found to be responsible for a high degree of residency (Itano and Holland 2000; Sibert and Hampton 2003; Schaefer et al. 2007). In these areas, the higher concentrations of prey in the vicinity of the archipelagos, islands and seamounts were thought to be the main driver of higher YFT abundance (Young et al. 2001; Morato et al. 2010). Mesoscale oceanographic features, such as fronts and eddies, that aggregate prey species, also impact YFT presence and catchability (Kai and Marsac 2010), as seen in the Mozambique Channel (Sabarros et al. 2009).

Spatial distribution, vertical behavior and habitat extent

Despite the importance of prey abundance at both local- and mesoscales, at large spatial scale, sea temperature is the most influential environmental variable driving YFT behavior and distribution (Schaefer et al. 2007). Although YFT's endothermic abilities allow its global distribution in tropical and sub-tropical waters, they spend most of their time either within the surface mixed layer or at the top of the thermocline (18 31 °C), where phytoplankton production is enhanced and epipelagic prey species are concentrated (Sund et al. 1981; Block et al. 1997; Brill et al. 1999; Reygondeau et al. 2012). Nonetheless, it is common practice to consider that body temperature (linked to endothermic and heat-

conservation strategies; see "Anatomical and physiological features" section) is the most important factor limiting YFT spatial distribution and vertical behavior. However, it is in fact the temperature of the heart that affects YFT movements. This organ is located on the "water" side of the vascular counter-current heat exchangers (Brill et al. 1998) and receives blood directly from the gills at ambient sea temperature (Brill and Lutcavage 2001). Falling sea temperatures result in a drop in heart rate, causing bradycardia and an associated reduction in cardiac output (Farrell et al. 1992). Moreover, at 15 °C, YFT have no capacity to increase their heart rates and cardiac output as the atropine that is used to reduce vagal nerve activity is inactive at that temperature (Brill and Bushnell 2001). Thus, YFT do not have the thermoregulatory physiological capacity to stay below the mixed layer for prolonged periods, explaining their daily-diving behavior (Brill and Lutcavage 2001; Galli et al. 2009). Rapid descents to depths deeper than 300 m with temperatures colder than 7 °C to chase prey or escape a predator have occasionally been recorded (Block et al. 1997; Dagorn et al. 2006; Hoolihan et al. 2014). In the EPO, Schaefer et al. (2009, 2011) recorded dives to 1600 m of depth as well as some repetitive bounce-diving behavior to depths of 200 400 m during the day.

In addition to sea temperature, dissolved O_2 concentrations can affect the vertical distribution of YFT. This is mainly linked to hemoglobin's affinity for O_2, a relationship which is strongly negatively influenced by elevated levels of carbon dioxide and reduced pH levels (Brill and Bushnell 2001). This has profound implications for respiratory gas binding and transport, especially in light of regional thermal differences (Graham and Dickson 2004). In particular, YFT's fast growth rate and high fecundity (see "Including biology into stock assessments" section) require higher O_2 delivery rates than those required for routine metabolic functions (Priede 1985). Therefore, YFT and other large pelagic fishes remain at depths where it is possible to find adequate levels of dissolved O_2 (i.e., within the oxygen minimum layer) to ensure those functions are maintained (Brill 1994; Prince and Goodyear 2006; Hoolihan et al. 2014).

The distribution and survivorship of YFT early life stages are more influenced by local environmental and oceanographic conditions than adults. Endothermic capabilities are acquired during the juvenile stage and

consequently, YFT larvae are confined to a much narrower range of habitats than adults (Reglero et al. 2014). During the yolk-sac stage, larvae are totally dependent on the presence of favorable biological and physical conditions (e.g., sea temperature and dissolved O_2) for survival (Margulies et al. 2001). The physiological thermal window for yolk-sac and first-feeding YFT larvae ranges between 21 and 33 °C (Wexler et al. 2011). Sea temperature is the primary determinant of the duration of this developmental stage, as well as key parameters that occur during this stage, such as the distribution and occurrence of the larvae, the duration of ingestion, metabolism and subsequent growth rates and mortality rates (Boehlert and Mundy 1993; Margulies et al. 2007; Sabatés et al. 2007; Wexler et al. 2007). In general, YFT larvae are found in all oceans with a sea temperature of higher than 24 °C and at depths less than 50 m and within the mixed layer (Wexler et al. 2007; 2011). Limiting physical conditions negatively influences the vertical and horizontal distribution of YFT larvae and as such, potential spatio-temporal overlaps with food and predators. Consequently, these conditions may negatively affect YFT larvae survival (Blaxter 1991). Finally, seawater density drives the development of the swim bladder, the organ that controls vertical migration during the larval phase (Wexler et al. 2011). It is noteworthy that post-larvae and small juveniles YFT (<30 cm FL) look very similar to related species, making morphological discrimination difficult and, therefore, catch misreporting could occur. This has prompted a number of studies aimed at using molecular markers to identify tuna species during early life history stages (for some example see Hyde et al. 2005; Viñas and Tudela 2009; Puncher et al. 2015) since it can affect estimates of species composition, particularly in multispecies fisheries that target juveniles tunas.

Yellowfin tuna fisheries

Global and regional fishery data

We retrieved global fisheries data for YFT from the following websites in January 2016: ICCAT, IOTC, WCPFC and IATTC; and also sourced data from inputs of stock assessment models. To merge the different data sets obtained from the four tRFMOs, we harmonized

the different data formats (i.e., species, fishing gear and flag state) in line with Food and Agriculture Organi-zation standards. Firstly, we used annual total catch (in MT; 1919 2015), available by fishing gear and flag state, to describe temporal changes in the magnitude of YFT catches over almost a century. We assumed total catch to be comprehensive and unbiased. It should be noted, however, that generally these values do not include tuna discarded at sea, and under- and misre-porting issues have been identified in some fisheries (Geehan and Pierre 2015). Secondly, we used spatially-aggregated catch data (by month; 1950 2013) to display global distributions of YFT catch by fishing gear over a full year. Spatially-aggregated catch data were mainly available for industrial fisheries and represented about 75% of the total catch over the period. Spatial data were raised to the total catch according to fishing gear and flag state after converting the catch, expressed in numbers of individuals, into biomass using ocean and gear-specific average weights. Data for the WCPO were only raised according to fishing gear as flag state information was not available. Thirdly, size distributions of the catch were used to describe the different life stages of YFT targeted by industrial fishing gears, as well as the conspicuous associative behavior of YFT with drifting floating objects. Indeed, fishermen have been taking advantage of this behavior to increase catches since the development of the purse seine fisheries (Greenblatt 1979). The biological meaning for this behavior still remains unknown (Freʹon and Dagorn 2000), but it appears to be size-dependent (i.e., small individuals show higher levels of association) and is known to influence YFT vulnerability to different fishing gears (Robert et al. 2012). Associations with other marine epipelagic species, such as whale shark (*Rhincodon typus*), whales and dolphins also occur in all tropical oceans (Capietto et al. 2014); although, fishing sets on schools associated with whale sharks and cetaceans are uncommon in most oceans and banned in some areas (e.g., in the IO, IOTC Resolutions 13/04 and 13/05 prohibit purse seiners setting on marine mammals and whale sharks, respectively). In the EPO, however, fishing sets on dolphins have been the dominant component of the purse seine fishery, contributing in average to about 60% of the total purse seine catches from 1960 to 2015 (Minte-Vera et al. 2016).

Catch-at-size matrices, derived from size-frequency samples, account for spatio-temporal distributions in

catch by fishing gear. Association school type and fleet were available for the periods 2001 2010 in the AO, 2005 2014 in the IO, 2006 2015 in the EPO and 2008 2014 in the WCPO. In absence of these matrices, length-frequency data from Japanese longliners operating in the southern EPO were used. We considered these data to represent the total EPO longline fishery well (C. Minte-Vera, pers. com.). A relative frequency distribution of catch-at-size values, representing an annual average, was considered to represent the recent decade. It was computed to compare size distributions between oceans for longline and purse seine sets on FSCs, associated with floating objects (including natural objects and artificial fish aggregating devices built by fishermen) and dolphin sets in the EPO. In the AO and IO, data did not include information on YFT discards, which are generally composed of fish ranging

from 30 to 50 cm FL (i.e., <1.5 2.2 kg; e.g., Chassot et al. 2014 for the IO) as well as YFT retained onboard and sold on the local markets of the main fishing ports of West Africa where it has been shown to be of minor importance as compared to SKJ for instance (e.g., Chavance et al. 2015).

History and development of YFT fisheries

The average global distribution of catch (1950 2013) indicates that YFT occur across most of the globe between 45°S and 45°N (Fig. 2). However, catch is mainly concentrated in the tropical waters of the eastern EPO (from Peru to the USA) and AO (from Angola to Mauritania), the western IO (from Mozambique to Somalia) and the WCPO (here, catch size appears to extend further eastwards than it does in the IO; Fig. 2).

The global shift in the YFT fishery from coastal to offshore has been driven by several factors, including improved gear and vessel technologies, market pressures associated with economic crises in some fisheries (e.g., the European sardine fishery) and, the large opportunities offered by an unexploited marine resource. In the 1950s, the sharp increase in demand for canned tuna drove a major change in the fishery. At this time, it was recognized that small-scale exploita-tion was operationally restrictive (i.e., only specific life stages and periods were accessible) and that this resulted in seasonal fluctuations in catch levels. Large
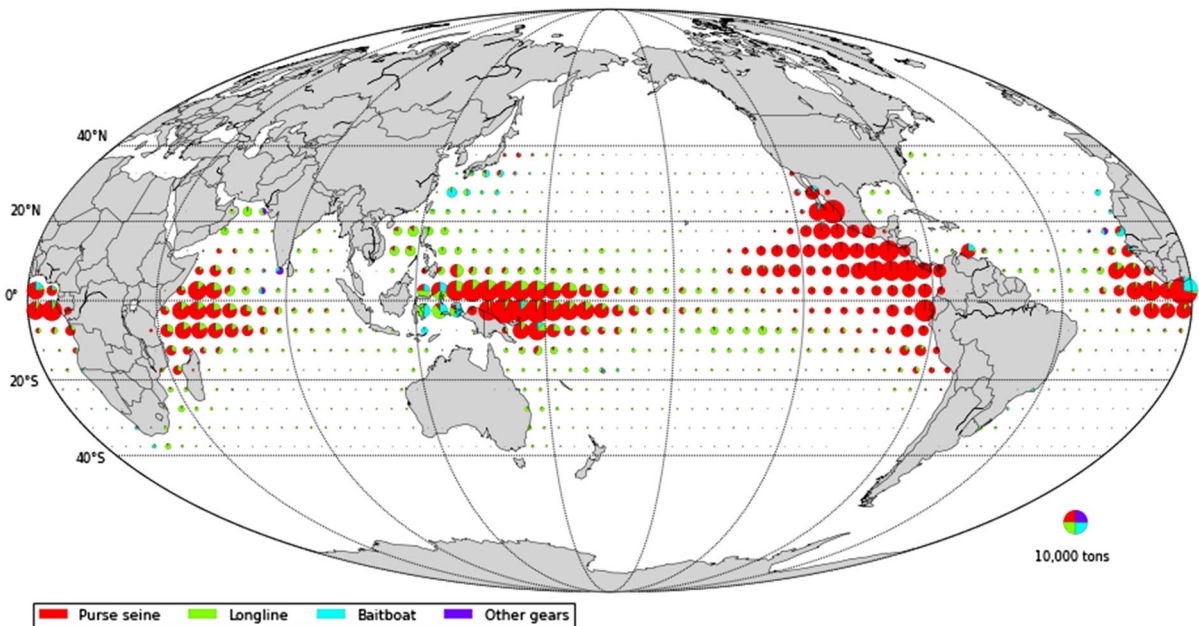
Fig. 2 Mean annual distribution of global yellowfin tuna (*Thunnus albacares*) catch by fishing gear type from 1950 to 2013. *BB* baitboat, *LL* longline, *PS* purse seine, *OTH* other gears.

For visualization purposes, the diameter of the pie is proportional to the square root of the catch.

industrial baitboats, longliners and purse seiners, all equipped with refrigeration systems, began to be built in the early 1950s. In response, the fishery expanded rapidly to exploit YFT over its full distribution (Fonteneau 1997, 2010). YFT landings steadily increased from less than 300,000 MT in the 1960s to about 1.5 million MT in the mid-2000s. In 2007, these values declined sharply to about 1.1 million MT (Fig. 3). In 2014, global YFT catch was around 1.4 million MT. Over the last decade, YFT has made up one fourth of global tuna catch, with an annual average catch of approximately 1.25 million MT (Fig. 3).

The magnitude of YFT catch has varied strongly between oceansover the last few decades. In the EPO, YFT has been harvested since the early 1900s by surface gears and live-bait fishing. This catch supplied American canneries, mainly based in California, where YFT were processed as light meat tuna. From the late 1950s, extensive changes took place in the EPO fishery, most notably the rapid expansion of longliners. Initially, this group was dominated by Japanese vessels (Broadhead 1962; Suda and Schaefer 1965; Fig. 3) which mainly targeted BET, while YFT has always been considered to be a secondary species for Japanese longliners operating in the EPO. The Japanese market for 'tuna sausage' increased rapidly since 1955 (Miyake et al. 2010) and this increased the attractiveness of the EPO for longliners. As a consequence, Japanese longliners, together with new vessels from the Republic of China, the Republic of Korea, and several other western hemisphere nations,

Fig. 3 Global yellowfin tuna (*Thunnus albacares*) catch by ocean basin from 1919 to 2014

expanded throughout the entire EPO. This resulted in a major increase in fishing effort in the following years (Shingu et al. 1974; Matsumoto and Bayliff 2008). During that same period, moreover, some of the baitboat capacity was transferred to large and new brand purse seine vessels, which were capable of catching larger numbers of YFT and operating further offshore. In 1977, coastal nations in the EPO extended their Economic Exclusive Zones, prohibiting foreign-flagged vessels fishing within their waters. This favored the development of South American flagged vessels, and this group now takes the largest percentage of YFT catch in the EPO. Purse seiners currently take more than 95% of the total YFT catch in the EPO (Minte-Vera et al. 2016).

The industrialization of the WCPO fishery started slightly earlier. Here, Japanese longliners began exploiting YFT in the late 1940s. From the early 1950s through the early 1960s, Japanese longliners established bases in Fiji, American Samoa, Vanuatu, New Caledonia and French Polynesia. These vessels mostly targeted albacore tuna (*Thunnus alalunga*), supplying canneries based in the USA (Gillett 2007). In the early 1960s, new longline fleets from Taiwan and South Korea developed and expanded while new baitboat fishing bases were established in western Pacific countries such as Palau, Pago Pago, the Solomon Islands and Fiji (Felando 1987). In the 1980s, the success of the WCPO purse seine fishery (in addition to issues occurring in the EPO, such as the strong El Niño event in 1982 1983 and public concerns regarding associated dolphin mortality) drove further expansion in the WCPO (Felando 1987). Since then, YFT landings have increased substantially from 105,000 MT in 1971 to more than 550,000 MT in 2000, peaking at more than 600,000 MT in 2008 (Fig. 3). Currently, the WCPO accounts for more than one-quarter of all YFT landings. The WCPO purse seine fishery was, moreover, responsible for almost 60% of global YFT landings in 2014 (i.e., about 610,000 MT; Fig. 3).

The tuna fisheries in the IO have some of the longest histories in the world. This is particularly true in the Maldives where skipjack tuna has been targeted for more than 700 years (Adam 2004). The development of an industrial YFT fishery in the IO dates back to 1952 when longliners started operating in the eastern region. Initial substantial YFT landings were large and encouraged new and large vessels to be built.
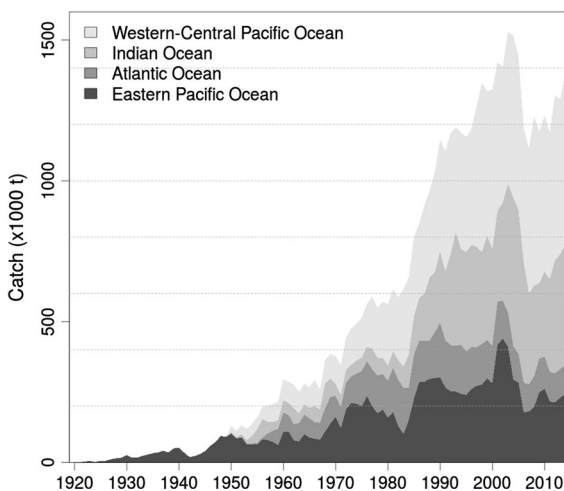
Exploitation in the western region began in 1954, and by the 1960s, most areas in the IO were being exploited. This gradual expansion was led by Taiwanese and South Korean longliners. While industrial fisheries landings of YFT catch in the IO are significant, artisanal fishers account for more than 50% of the total catch. The total annual IO YFT landings increased from about 50,000 MT in the mid-1950s, to more than 70,000 MT in the early-1980s. During this time, longlines were the dominant gear type (Fig. 3). Meanwhile, several exploratory cruises by Japanese, Mauritian, and French purse seiners were conducted in both the east and west IO from the very late 1970s to the early 1980s and marked the start of the PS fishery in the region. Later, many other European purse seine vessels arrived from the AO, an area where catch rates were starting to decline due to the anomaly associated with El Niño during the first quarter of 1984. This expansion was supported by an increase in fishing efficiency due to the development of modern equipment (e.g., bird radars) and the increasing use of support vessels and fish aggregating devices (FADs) (Miyake et al. 2010). YFT landings increased throughthe 1990s, reaching over 400,000 MT in 1993 and fluctuating around that level until 2002 (Fig. 3). From 2003 to 2006, YFT landings increased further, with an average annual catch of approximately 480,000 MT, peaking in 2004 at over 525,000 MT. After that, landings decreased noticeably. In areas off Somalia, Kenya and Tanzania, this decrease in YFT landings has been due to the indirect effects of local piracy (Chassot et al. 2010). Between 2009 and 2011, the decline in YFT landings was less marked in the purse seine fleet than for the longline fleet due to the presence of armed personnel onboard since 2009 (Chassot et al. 2010). The effort of all fleets has, however, significantly increased in recent years, to about 415,000 MT in 2014 (Fig. 3). In 2014, purse seines were the main gear type, accounting for 33% (∼150,000 MT) of the total YFT landings.

In the AO, YFT are caught in tropical and subtropical waters between 45°N and 40°S. The expansion of the longline fishery in the AO started in 1957, in parallel to the extensive exploitation and subsequent decrease of YFT catches in the IO. This drove the Japanese, Taiwanese and Korean longline fleets to relocate their effort to other areas, with consequent increases in YFT landings. Although the number of longline vessels increased after the late 1960s, the

Japanese longliners switched their target from YFT to BET in the mid-1970s, while the Taiwanese fleet, after a short period (∼2 3 years) harvesting YFT, quickly switched to albacore.

At the same time, a baitboat fishery was developed in the eastern AO from the mid-1950s by French and Spanish vessels. Later, a Japanese fleet based in Tema (Ghana) and operating in the Gulf of Guinea, joined them (Le Guen et al. 1965). The efficient activity of most baiboat fleets in the eastern AO was a direct consequence of the new bait-fishing mode of the Dakar baitboat developed since the early eighties, where the baitboat associated and aggregated the tuna schools underneath acting as a fish aggregating device (Fonteneau and Diouf 1994). Although some Senegalese, Spanish, and Ghanaian baitboats are still operating in West African waters and around the Canary Islands, this fishery has declined strongly in the 1980s and 1990s due to poor economic performance. Overall, YFT dominated AO tuna landings until the 1990s, exceeding 190,000 MT (Fig. 3). Since then, YFT catch has started to decline as fishing effort decreased, and has been replaced by skipjack tuna. In the last few decades, however, YFT catch by the purse seine fishery has increased very quickly and now accounts for about 70% of the total AO YFT catch, with annual values of 70,000 MT.

Globally, baitboats dominated the YFT fishery until the early 1950s when the industrial longline fishery developed and rapidly expanded worldwide (Fig. 4).
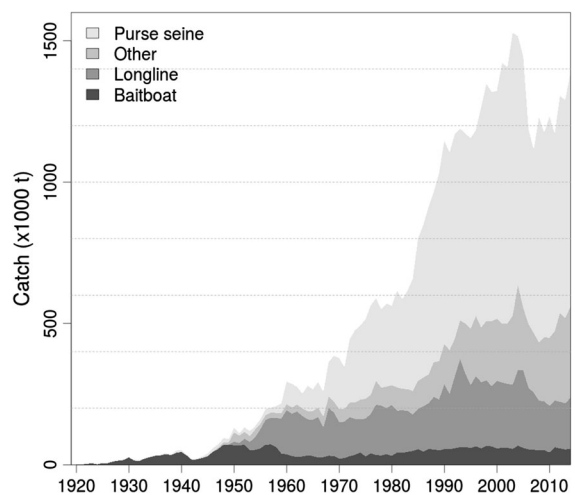
Fig. 4 Global yellowfin tuna (*Thunnus albacares*) catch by fishing gear type from 1919 to 2014. *BB* baitboat, *LL* longline, *PS* purse seine, *OTH* other gears
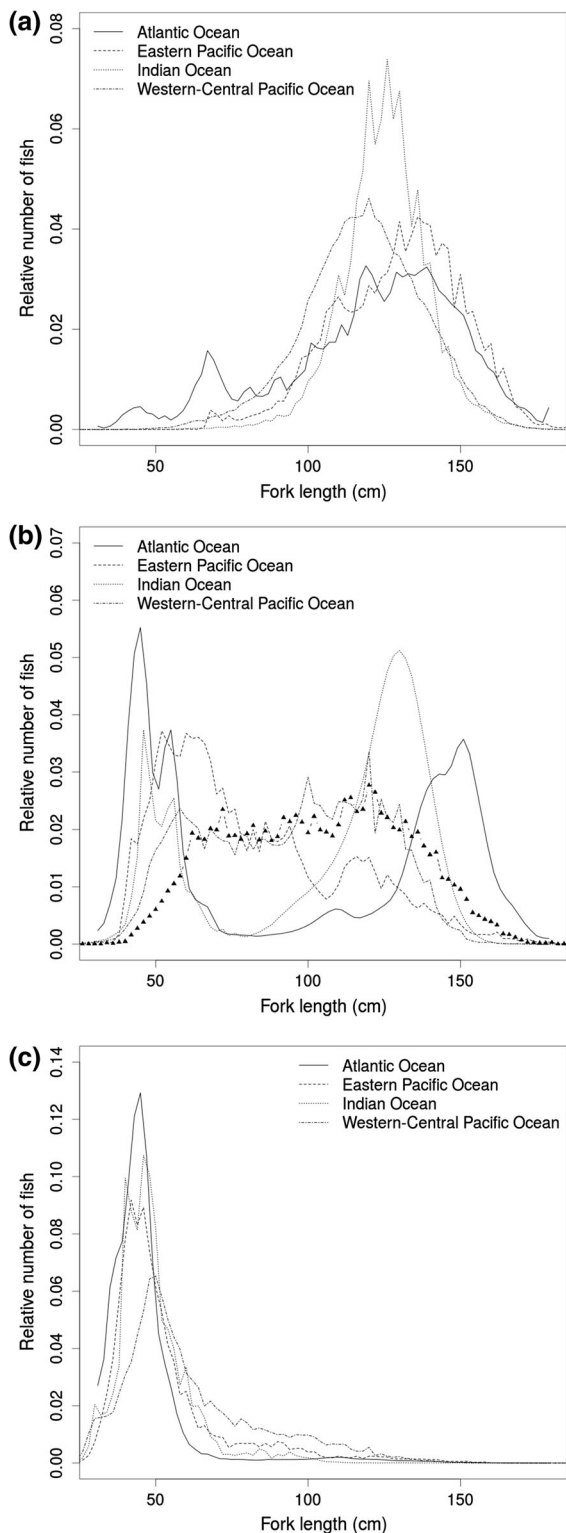
(a)

(b)

(c)

The contribution of baitboats landings has declined from 80% in 1949, to less than 10% in the late 1960s (Fig. 4). In the 1960s, the longline fishery represented almost 50% of YFT catch, but its importance started to decline with the advent of large purse seiners. At that time, the latter were capable of landing up to 1500 MT annually, rising to more than 3000 MT by the 1970s. Since the early 1980s, purse seiners represented about 60% of the global YFT catch and now is the dominant gear type used to harvest YFT (Fig. 4).

Large uncertainties surround the size and composition of tuna catches by small-scale and semi-industrial fisheries. These fisheries mostly support local markets but ensure the food security of millions of people. In the last decade, they have been estimated to account for around 20% of the global YFT catch; although, the true proportion is thought to be even higher (Pauly and Zeller 2016). For example, in the IO, a recent sampling program in Indonesia indicated that juvenile tunas caught by small-scale fisheries were being widely misidentified, suggesting that the quantity of YFT landings is being significantly underreported.

YFT fishing patterns and associative-behavior

The size distribution of YFT caught by industrial fleets differs significantly between gear type and ocean. Longliners mainly target adult YFT (>100 cm FL) and during the 2000s, overall fishing patterns are similar between oceans (Fig. 5a). For large individuals, the size distribution is very similar between the AO and EPO (Fig. 5a). YFT caught on longlines in the WCPO have a size mode of approximately120 cm FL, while in the IO, their distribution centers around 130 cm FL (Fig. 5a). The size distribution of YFT is wider in the AO and EPO where the proportions of large individuals (>140 cm FL) are higher than in the WCPO and IO (Fig. 5a). For purse seiners fishing on

FSCs, size distributions are more complex, with large differences observed between oceans. Size-frequency histograms showed two distinct modes for small and large YFT in the IO and AO (Fig. 5b). Size modes are very similar for YFT smaller than 80 cm FL (size range 40 60 cm FL) while for larger individuals, the size mode is130 cm FL in the IO and 150 cm FL in the AO (Fig. 5b). In contrast, the size distribution of YFT on unassociated schools in the EPO does not show any mode for large individuals but a decreasing trend, with sizes ranging from 50 to 70 cm FL. In the WCPO, purse seine fishing on FSCs mainly captures individuals between 50 and 130 cm FL, with the distribution showing an upward shift from 50 to 90 cm FL to 100 130 cm FL (Fig. 5b). YFT caught with dolphins in the EPO have an overall size distribution similar to that of YFT caught on FSCs in the WCPO, but are shifted forward by 10 cm FL (Fig. 5b). Finally, individuals caught on floating objects are mostly smaller than 60 cm FL (i.e., about 4.5 kg) and their size distribution appear very similar between the IO, AO and EPO during the 2000s, with a mode of 40 cm FL (Fig. 5c). YFT caught on floating objects in the WCPO appear to be a bit larger, with a mode of 50 cm FL (Fig. 5c).

Management of YFT stocks

YFT is currently managed at an ocean basin scale by the tRFMOs. Consequently, each ocean is considered to have a single stock (i.e., four distinct stocks occur in the AO, IO, WCPO and EPO). This management approach simplifies the complex biological and ecological processes we have thus far described, despite their involvement in shaping population dynamics and structure. The current status of the four stocks is based on the last stock assessments carried out by the scientific bodies of each of the tRFMOs. The main objective of these assessments is to estimate stock parameters; for example, time series of recruitment, biomass and fishing mortality, all in relation to biological reference points. The stock status is estimated through different demographic models that range from simple surplus production models to complex age-structured mod-els, which can account for movements between large areas when sufficient movement information is available.

Including biology into stock assessments

Biological information is currently integrated into YFT stock assessment models through the vectors at-age and (or) at-length of weight, growth, natural mortality, sex-ratio and maturity.

Age and growth

The estimation of YFT age and growth is challenging for three reasons: (1) the hard pieces used in fish aging (e.g., otoliths) are less marked in tropical environments as compared to temperate waters, (2) despite some seasonality in spawning, reproduction occurs year round, which makes it difficult to interpret otolith readings, and (3) several biases and uncertainties are known to affect age estimates derived from reading micro-increments in otoliths (Sardenne et al. 2015). Different aging procedures have been used to determine YFT growth: (1) modal progressions in length-frequency distributions from commercial catches or scientific monitoring (Gascuel et al. 1992), (2) direct aging from periodic deposits in calcified structures (i.e., scales: Yabuta et al.1960; dorsal spines: Lessa and Duarte-Neto 2004; and otoliths: Stéquert et al. 1996) and (3) length increments derived from mark-recapture experiments (Bard 1984). More recently, integrated modeling approaches have been developed to combine different data sources within a unifying statistical framework to estimate growth in IO YFT (Dortel et al. 2015; Eveson et al. 2015).

Although YFT growth was first modeled using the von Bertalanffy (1938)'s model (Yang et al. 1969; Le Guen and Sakagawa 1973), growth studies conducted over the last few decades have generally supported a two-stanza growth model with a significant change in the growth rate between juveniles and adults (Fonteneau and Chassot 2013). This model considers two distinct growth phases. In the IO, a first phase occurs in young YFT, which shows a slow growth rate (~ 2 cm month^{-1}) until they reach 56 70 cm FL (Dortel et al. 2015; Eveson et al. 2015). A second, faster growth phase (~ 4 cm month^{-1}) occurs when YFT reach approximately145 cm FL, with a progressive decrease of the growth rate with size thereafter (Fig. 6a). The two-stanza growth model could be physiologically explained using the different metabolic requirements relative to YFT size, the development of the swim bladder and reproduction. This
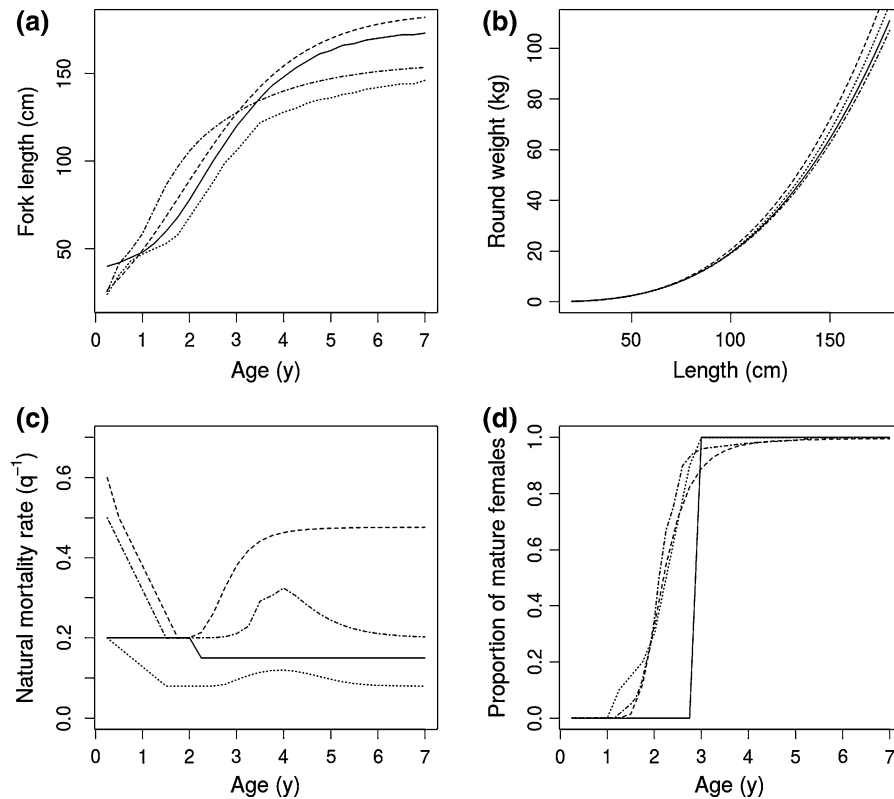
Fig. 6 Biological parameters currently used in stock assessment models of yellowfin (**a**) growth curve, (**b**) length weight relationship, (**c**) natural mortality rates, (**d**) proportion of mature females. Each Ocean is represented by a different line type: Atlantic Ocean (*solid*); Indian Ocean (*dotted*); Eastern Pacific Ocean (*dashed*); Western Pacific Ocean (*dotdash*)

interpretation was also stressed by Lumineau (2002), who suggested that the lower metabolic rate of large individuals and the development of the swim bladder could drastically reduce the energy required to swim. In fact, the swim bladder grows allometrically in YFT and does not contain gas until fish reach 50 60 cm FL. This implies that after this size, individuals have higher amounts of energy available for growth. The development of the swim bladder is, moreover, associated with increased size allows YFT to swim deeper, increasing their capability to catch prey (Lehodey and Leroy 1999; "Feeding strategy" section). Even if a two-stanza growth model has been confirmed in different oceans (Fonteneau and Hallier 2015), there is still some debate about the functional form of the resulting growth curve, as some YFT aging studies have resulted in typical Von Bertalanffy growth (Driggers et al. 1999; Shuford et al. 2007). Some authors have suggested that the two-stanza growth curve could stem from the particular

selectivity of purse seines, the main gear fishing used to harvest the catches from which the tagged tunas were recovered. Simulation studies and integrated growth models (including tagging, otolith and size-frequency data) both, however, indicate that gear selectivity alone cannot explain the complex growth pattern observed in tunas (Dortel et al. 2015; Eveson et al. 2015).

The age-length relationship in YFT changes between oceans, especially after 3 years of age. The highest length values (for the same age) were recorded in the EPO (Fig. 6a). Sexual dimorphism in growth has been highlighted in YFT, with an increasing proportion of males making up the larger size classes in all oceans (Capisano 1991; Schaefer 1998). In the IO, males become dominant at the 145 154 cm FL size class (Nootmorn et al. 2005; Zhu et al. 2008; Zudaire et al. 2013b) while females dominate the 115 130 cm FL size class (Nootmorn et al. 2005; Zudaire et al. 2013b). These results corroborated those

reported by Stéquert et al. (1996) for the IO, indicating a size discrepancy between the two sexes. In this study, males were found to be larger than females at 3 and 4 years old (120.4 vs. 118.0 cm FL and 146.5 vs. 142.2 cm FL, respectively). The majority of males were reported to be larger than 135 cm FL in the EPO (Schaefer 1998) and 138 cm FL in the WCPO (Sun et al. 2005), while in the AO most males were larger (144 172 cm FL; Diaha et al. 2015). These variations could be the consequence of differences in growth rate or sex-dependent mortality (natural and fishing) (Timochina and Romanov 1991; Fonteneau 2002). A higher natural mortality rate was observed in females >130 cm FL as compared to medium sized individuals (Hampton and Fournier 2001), possibly linked to the high energetic demands of spawning (Schaefer 1996). Despite the strong evidence for sexual-dimorphism in YFT growth, current stock assessments do not incorporate this distinction.

Natural mortality

Natural mortality (M) is one of the most important parameters in stock assessment as it determines the productivity of the stock and, hence, its resilience to fishing. It is however very difficult to estimate and generally fixed at different values for sensitivity analysis. The use of different natural mortality vectors greatly influences the resulting stock status from stock assessment and, ultimately, the management advice provided. Natural mortality includes predation-related mortalities, as well as those from other sources, such as disease and senescence. In tunas, the relationship of M to body size/age is generally assumed to decrease or follow a U-shaped relationship (Hampton 2000) although values of M collated from YFT most recent assessments show a high variability between stocks (Fig. 6c). Data collected from mark-recapture experiments provide some information on M, and these data sets (when they are available) are now included in YFT assessments. It remains, however, difficult to untangle the contribution of M to the total mortality affecting tuna stocks when selectivity patterns are estimated and assumed to change over time and space. In addition, low recovery rates of tagged individuals from some tuna fisheries (e.g., longliners) bias estimates of M (Carruthers et al. 2014), while the time required for complete mixing of tagged individuals into the population in IO prevents the estimation

of M for YFT juveniles (Kolody et al. 2016). When tagging data are not available, M at age is generally estimated from empirical models that are based on life history invariants (Lorenzen 1996; Gislason et al. 2010). In stock assessments, M is generally considered to be constant over time, but assumed to vary with fish size or age. The different values of M used in the stock assessments of YFT across the three oceans in conjunction with information on recruitment (i.e., steepness) and growth (Fig. 6c) have an influence in the resulting status of the stock. For example, the differences of M vector after 2 years of age, become very noticeable between the Pacific and the other two oceans, with lower and more constant values reported in AO and IO (Fig. 6c). This entails that a lower productivity for YFT in the AO and IO is assumed and, hence, that the YFT in the AO and IO would be more prone to overfishing.

In the larval stages, high values of M (due primarily to starvation and predation) have been shown. Estimates of total mortality rate during larval development have been measured from declines in abundance over time (Hampton 2000). Lang et al. (1994) estimated a total mortality of 0.33 d^{-1}, a figure which may also be related to feeding and nutrition during these early stages. Current information indicates that the M during the early life stages of tunas is, however, largely a function of size or age rather than species. For instance, small YFT and BET living in mixed schools in the same habitat and in very close association, face the same food availability and risk of predation; and as such should suffer similar levels of natural mortality (Hampton 2000; Fonteneau and Pallarés 2005).

Reproductive strategy and maturity

YFT is an iteroparous, gonochoristic and oviparous species that does not display sexual dimorphism in its external morphology. Fertilization of eggs occurs externally and there is no parental care. Oocyte development pattern is asynchronous (Schaefer 1998, 2001; Zudaire et al. 2013a) and fecundity regulation strategy is indeterminate (Zudaire et al. 2013a). Oocytes are continuously produced and recruited in the ovary throughout the spawning season, moving from a primary growth stage through to the maturation stages. As such, an overlap occurs between oocyte recruitment and spawning events (Schaefer 1998; Zudaire et al. 2013a). The size and/or age at

which individuals mature is an essential life history trait for YFT stock assessment (Schaefer 2001). The size at which 50% of the YFT population (L_{50}) reaches maturity varies between oceans, and in response to relevant environmental cues (Fig. 6d). In females, this size is estimated to be 75 114 cm FL in the western IO (Zhu et al. 2008; Zudaire 2013b), 92 cm FL in the EPO (Schaefer 1998), 104 108 cm FL in the WCPO (McPherson 1991a, b; Itano 2000) and 103.7 109 cm FL in the western AO (Albaret 1976; Diaha et al. 2015) (Fig. 6d). It is thought that the reduced productivity in the WCPO may be driving the later maturation of individuals there, as compared to the EPO (Schaefer 1998; Sun et al. 2005). It also appears that there may be a delay in maturity at higher latitudes, which is thought to be related to lower sea temperatures (Itano 2000). There are also differences between the two sexes, with females measuring 92 cm FL and males 69 cm FL at L_{50} in the EPO (Schaefer 1998) and 97.2 cm FL for females and 76.3 cm FL for males in the western AO (Frank et al. 2015). In general, the lack of standardized criteria for estimating maturity (e.g., there is no established threshold for determining maturity based on specific oocyte development stages) and the use of different methods (i.e., microscopic vs. macroscopic) make comparisons difficult within and between oceans (Itano 2000; Schaefer 2001) (Table 1). In the majority of L_{50} studies completed to date, YFT females have been considered to be mature when they displayed advanced vitellogenic oocytes. However, this threshold could lead to exaggerated maturity estimates because it classifies maturing individuals (i.e., individuals with cortical alveolar stage oocytes; CA) as immature (Zudaire et al. 2013b). The CA stage represents the earliest evidence of oocyte maturation (Brown-Peterson et al. 2011), and as such, females with ovaries in this stage should be considered in maturity estimates (Lowerre-Barbieri et al. 2011). Following this recommendation, L_{50} for YFT females has been estimated to be 75 cm FL in the western IO (Zudaire et al. 2013b), 103 cm FL in the eastern AO and 97.2 cm FL in the western AO (Diaha et al. 2015; Frank et al. 2015). In contrast, when the maturity threshold has been defined by the presence of advanced vitellogenic oocytes, these estimates increased to 102 cm FL in the western IO and 118.8 cm FL in the eastern AO (Zudaire et al. 2013b; Diaha et al. 2015).

Spawning and fecundity

Female YFT have a protracted spawning period during which time mature oocytes are released in multiple batches, with spawning frequency of 1.1 1.5 days (Table 1) throughout much of the tropical zone (Itano 2000; Schaefer 1998, 2001; Zudaire et al. 2013a). This spawning activity is temperature-dependent (24 ° C and above; Schaefer 1998) and mainly occurs at night (McPherson 1991a, b; Schaefer 1996) or in the early hours of the morning (Itano 2000) between 21:00 and 3:30. Captive YFT have, however, been observed to spawn in the afternoon or evening (from 13:30 to 21:30) coinciding with higher seawater temperatures (Margulies et al. 2007). Diel activity is also related to hatching and egg-stage duration, which are likewise inversely related to the seawater temperature (Margulies et al. 2007). This pattern may be an adaptive trait to increase the chance of survival of newly hatched YFT larvae. YFT spawning behaviors are affected by ocean, hemisphere, and environmental conditions. In broad terms, the spawning period lasts between four and six months, occurring from November to February in the western IO (Stéquert et al. 2001; Zudaire et al. 2013b), from December to April in the eastern AO (Diaha et al. 2015), from May to September in the western AO and from April to October in the WCPO (Itano 2000) (Table 1). Globally, strong intra-specific variability of YFT fecundity has been reported, with global batch fecundity estimated to be between 1.6 and 3.1 million oocytes per batch, and a global relative batch fecundity between 55 and 74 oocytes per gram of body weight (Table 1).

Spawning and fecundity in YFT are highly dependent on the amount of energy invested in offspring by mature females who have to balance their surplus energy (energy available above the maintenance level) between somatic and gonadal growth (i.e., reproduction) (Rijnsdorp 1990). While tropical fish with indeterminate fecundity are generally defined as income breeders who use their recent energy intake for their current reproductive investment, some studies suggest that female YFT in the western IO employ a mixed income-capital breeding strategy (Zudaire et al. 2014, 2015). For those fish, gonad development relies first on the energy provisioned by concurrent feeding during the protracted spawning period. Spawning, however, may also depend on the relative food availability, as accumulated energy reserves stored

Table 1 Length at 50% maturity (L5; [a]: cortical alveoli; [b]: vitellogenesis; NR: not reported), the method for estimating it (Mac: for macroscopic; Mic: for microscopic), the spawning season and its frequency in days

Area	Sub-area	L50	Method	Spawning season	Spawning frequency (days)	BF	BFrel	References
EAO	Gulf of Guinea	109	Mac	December–April	NR	NR	NR	Albaret (1976)
WCPO	Coral Sea	105[a]	Mic	October–February	1.54	NR	NR	McPherson (1991a, b)
EPO	Clipperton atoll	NR	Mic	NR	1.14	1.57 (0.5–3.5)	68.0 (36.0–99.7)	Schaefer (1996)
EPO	Different sub-areas	92[a]	Mic	Throughout the year	1.52	2.50 (0.1–8.0)	67.3 (4.9–174.0)	Schaefer (1998)
WPCO	Different sub-areas	104.6[a]	Mic	Throughout the year	1.99	2.16 (0.4–10.6)	54.7 (31.9–147.1)	Itano (2000)
AO	Gulf of Mexico-Caribbean Sea	NR	Mic	March–November	3.35	2.16 (1.26–4)	54.2 (34.6–94.8)	Arocha et al. (2001)
IO	Western sub-areas	NR	NR	December–March	NR	NR	NR	Stéquert et al. (2001)
WCPO	Different sub-areas	107.77[a]	Mic	February–September	1.69	2.71 (0.9–4.7)	62.1 (31.0–98.0)	Sun et al. (2005)
IO	West-Central sub-areas	113.77[a]	Mac	January–June	NR	NR	NR	Zhu et al. (2008)
IO	Western part	75[b] 102[a]	Mic	November–February	NR	3.10 (0.32–6.91)	74.4 (9.2–180.8)	Zudaire et al. (2013b)
WAO	Gulf of Mexico	68.5[b]	Mic	May–September	1.16	NR	NR	Brown-Peterson et al. (2013)
WAO	Gulf of Mexico	97.2[b]	Mic	April–August	1.70	0.35 (0.04–1.18)	NR	Frank et al. (2015)
EAO	Gulf of Guinea	99.3[b] 115.1[a]	Mic	December–April	NR	2.91 (0.6–7.5)	54.4 (12.7–125.6)	Diaha et al. (2015)

Batch fecundity (BF) and the relative batch fecundity (BFrel) and the values are expressed in millions for BF and in oocytes per gram of gonad-free weight for BFrel. For each BF and BFrel estimates, the minimum and maximum values are also reported

as lipids in the liver can be used for oocyte recruitment (Zudaire et al. 2014). Finally, fish size and age can also affect YFT reproductive potential, with larger females showing a higher spawning fraction in the EPO (Schaefer 1998) and a longer spawning period in the western IO (Zudaire et al. 2013b). But further studies are needed to confirm this hypothesis.

The energetic cost associated with spawning also varies according to gender, with higher energy investments required for eggs (around 1% of body wet weight per spawning event) than for sperm (Schaefer 1996, 1998). In contrast to female YFT, our current understanding of male reproductive biology is poor. This limits the ongoing assessment and management of YFT worldwide. There is also an obvious knowledge gap in our understanding of chromosome and karyotype features that are needed to understand YFT reproductive biology. Our current understanding indicates that there are no morphologically-differentiated sex chromosomes in YFT, as is the general case for the genus *Thunnus* (Ratty et al. 1986; Soares et al. 2013).

Fecundity and both the timing and duration of spawning periods are currently not accounted for when estimating reproductive potential in YFT stock assessments. Instead, reproductive potential, which is based on the stock recruit relationship, is traditionally measured using an estimate of the spawning stock biomass (Trippel 1999; Lowerre-Barbieri et al. 2011). This parameter implies that the survival rates of offspring are independent of parental age, body size or condition (Cardinale and Arrhenius 2000), and moreover, that the total relative egg production per unit weight of adult stock is invariant over time (Morgan et al. 2009), although this is unlikely to be the case (e.g., Marshall et al. 2010).

Thus, fecundity is only related to the mass-at-age of the sexually mature portion of the stock, irrespective of the demographic composition of adults (Kell et al. 2015).

Current status and management

The status of tuna stocks are currently set relative to MSY-based reference points [e.g., the ratio between the current spawning stock biomass and the spawning stock biomass at MSY (B/B_{MSY}) and the ratio between fishing mortality and fishing mortality at MSY (F/F_{MSY}) (Table 2)]. YFT in the EPO is the stock with the longest history of assessments among tuna and tuna-like species, with the first evaluation taking place in 1962. In the most recent YFT stock assessment carried out in the EPO (Minte-Vera et al. 2016), an integrated statistical age-structured stock assessment model was used, indicating that: (1) the stock has experienced two, or possibly three, different recruitment productivity regimes in the last 40 years (1975 1982, 1983 2002 and 2003 2012); although these might result from the expansion of fishing grounds over time (Die et al. 1990); (2) the MSY was stable for the entire assessment period (1975 2014) while the overall level of fishing effort changed in respect to that MSY level, and, (3) the biomass in 2015 was estimated to be larger than B_{MSY} and fishing mortality was below F_{MSY}.

The YFT stock assessment in the WCPO has a more recent history, with the first annual assessment conducted in 1999 and the last one in 2007 (Hampton et al. 2004, 2005, 2006; Langley et al. 2009, 2011). YFT are considered to constitute a single stock within the WCPO (Hampton and Fournier 2001). The method-ology used for the 2007 stock assessment (Table 2) was based on a length-based, age-structured model (MULTIFAN-CL). This model provides an integrated method for estimating catch-at-age composition, growth parameters, mortality rates, recruitment and other parameters from time series of fishery catch, effort and length frequency data (Hampton and Fournier 2001; Davies et al. 2014). The stock assess-ment carried out in 2007 indicated that the WCPO YFT stock was not overfished, with spawning biomass above the B_{MSY} and fishing mortality below F_{MSY} (Table 2). Catches, however, approached or exceeded MSY (WCPFC 2014).

The most alarming situation concerns the status of the YFT stock in the IO. This stock was determined to be overfished and subject to ongoing overfishing during the last assessment (IOTC 2015). The low level of stock biomass observed in 2014 aligns with the long-term decline seen in the primary stock abundance indices (i.e., longline CPUE indices). This decline was driven by increased effort from longliners, gill nets, hand lines and purse seiners, and a rise in their associated landings in recent years. Consequently, fishing mortality exceeded the F_{MSY}, and in 2014, the spawning biomass was estimated at 23% (21 36%) of unfished levels and at 66% (58 74%) of the biomass corresponding to MSY (Table 2). A new assessment in 2016 has been requested by the Commission to

Table 2 Key fisheries parameters currently reported for yellowfin tuna (*Thunnus albacares*) by each of the tuna Regional Fisheries Management Organizations (tRFMOs): the most recent total catch (in metric ton), the average yearly catch in metric ton from the 5 years preceding the last stock assessment (5 year catch in metric ton), the maximum sustainable yield (MSY) and the reference point for fishing mortality (F; F/FMSY)

	Estimate	Years		Note
WCPFC				
Recent catch (mt)	599	2014		7% > 2013
5 year catch (mt)	565	2010	14	
MSY	586.00	2008	11	
F/FMSY	0.72 (0.58 0.90)	2008	11	F < FMSY
B/BMSY	1.24 (1.05 1.51)	2012		B > BMSY
IATTC				
Recent catch (mt)	243	2015		0.1% > 2014
5 year catch (mt)	229	2011	2015	
MSY	272. 84	2012	2015	
F/FMSY	0.94 (0.59 1.46)	2012	2015	F < FMSY
B/BMSY	0.93 (0.79 1.02)	2015		B ≤ BMSY
ICCAT				
Recent catch (mt)	104	2014		3% > 2013
5 year catch (mt)	106	2010	2014	
MSY	145 (114 155)	2010		
F/FMSY	0.86(0.68 1.40)	2010		F < FMSY
B/BMSY	0.96 (0.61 1.12)	2010		B < BMSY
IOTC				
Recent catch (mt)	430	2014		6% > 2013
5 year catch (mt)	373	2010	2014	
MSY	421 (114 155)	2014		
F/FMSY	1.34 (1.02 1.67)	2014		F > FMSY
B/BMSY	0.66 (0.58 0.74)	2014		B < BMSY

monitor the status stock using update CPUE indices as well as nominal catches.

In the AO, the last YFT stock assessment was conducted in 2011. This assessment was based on the available catch data up to 2010, employing both age-structured (VPA) and biomass dynamics (ASPIC) models. The AO stock is considered to be overfished (i.e., the stock biomass is below B_{MSY}); however, fishing mortality was estimated to be below F_{MSY} (Table 2), meaning that overfishing is not occurring.

A crucial step toward improving the assessment of YFT stocks is to define their geographic boundaries, or stock units. This continues to be an issue characterized by uncertainty both within and between the tRFMOs. In this context, it is crucial that stocks are assessed with all the scientific and technological tools available in order to avoid mismanagement. Progress, moreover, is needed to improve data collection, the adaption of reference points, and the development of the harvest control rules (HCRs). These rules are a set of well-defined management actions that are made in response to changes in a stock's status, with respect to target and limit reference points. The adoption of HCRs is a crucial aspect of modern fisheries management. At present, none of the tRFMOs make any explicit statements on how to achieve targets or avoid limits; statements that could be interpreted as HCRs. Although relevant frameworks for the development of these reference points and HCRs have been already developed within tRFMO documents (some examples are the CMM 2014-06 adopted by WCPFC, the Resolution 15/10 by IOTC and the Recommendation 11 13 given by ICCAT), the adoption of such measures is slow. Currently, most of this work is conducted at the scientific level, without formal mandate from the tRFMOs. The tRFMOs would also need to evaluate proposed HCRs under their management strategy evaluation process. This process would ensure that proposed HCRs would be tested for robustness against stock reference points and assessed

for benefits and risks to ensure that they would contribute to sound stock assessments and management advice. From an integration perspective, however, it is important to note that this process differs between the four tRFMOs. Further, these management procedures are generally developed and integrated at the scientific level, with little or no feedback from stakeholders and commissioners.

Tagging studies

Mark-recapture studies using conventional identification tags and the more recent studies employing electronic tags have enhanced our understanding of YFT movements and stock mixing. The spatial structure of YFT stocks is, however, extremely hard to understand, as it is influenced by a multitude of biotic and abiotic factors (i.e., geographic features, oceanographic processes and prey availability). YFT are able to undertake long-distance horizontal migrations and show the highest mobility in the AO, where they have been shown to cover an average of 1600 nautical miles per month (Zagaglia et al. 2004). From the 18,210 YFT tagged by anglers off the eastern U.S. coast and recovered in the Gulf of Guinea, 45 individuals showed trans-Atlantic movements (Bard and Hervé 1994). Ranging in size from 40 to 135 cm FL, and with times-at-liberty ranging from 18 months to almost 10 years, each of these 45 individuals travelled an average of 4100 nautical miles (Fonteneau and Hallier 2015). These trans-Atlantic movements are part of a broader migratory pattern that is thought to be linked to natal homing (Zagaglia et al. 2004). Observations of YFT juveniles occupying the Gulf of Guinea until they reach the pre-adult stage (60 80 cm FL; age 1.5 2 years) further support this hypothesis. YFT juveniles start moving from the eastern to western AO to feed and grow. At the adult stage
(approximately 110 cm FL and ~ 3 years), YFT return to the eastern AO to spawn (Zagaglia et al. 2004). A higher degree of site fidelity and more restricted movements are suggested for YFT in the WCPO (Itano and Holland 2000; Sibert and Hampton 2003) and the EPO (Schaefer et al. 2007, 2011) than in the other oceans. For instance, a persistent seasonal cycle has been shown in YFT movements between central and northern Baja California, with northward movements observed in summer and southward movements observed in winter (Schaefer et al.

2007, 2011). Although tagging results from the EPO show large YFT movements (average distance travelled: ~ 710 nautical miles between 2002 and 2010), any assumption about complete mixing over large regional areas was excluded (Schaefer et al. 2011). This indicates that YFT exhibit higher levels of structuring and site fidelity within oceans than generally assumed by the tRFMOs (Sibert and Hampton 2003; Schaefer et al. 2009, 2011; Langley and Million 2012). The Regional Tuna Tagging Programme, which took place between 2005 and 2009, revealed fast and large-scale movements of YFT within the IO. This result supports the hypothesis of a single well-mixed YFT population in the IO. The great majority of the tags were, however, released close to the coasts of Tanzania and Mozambique and mostly recovered by purse seiners operating in the Western part of the IO, with very few recoveries from the eastern part. It remains however unclear if this result reflects low movement rates between the two parts of the IO basin or if it is due to low reporting rates from fisheries operating in the eastern IO (Langley and Million 2012).

Genetic population structure studies

As with tagging studies, genetic population structure studies have substantially contributed to our understanding of how tunas are structured into reproductively isolated populations. Since the 1970s, the continuous development of new molecular techniques has improved our capability to investigate DNA variations to address critical conservation and fisheries management issues, such as stock structure and population demography (Hauser and Carvalho 2008). Genetic results have provided new insights into the spatial dynamics, migratory movements and population structure of YFT (and other tuna and tuna-like species). Such information is crucial for the development of effective management strategies because local populations represent different evolutionary units due to their unique contributions to overall genetic diversity. Local populations are, moreover, adapting to different environmental conditions and are being exploited by different fishing gears. These localized pressures mean that each population unit can be characterized by exclusive, genetically-based morphological, physiological and life history traits, and therefore have unique conservation issues.

Despite YFT's biological and economic importance, and the general increase in genetic studies over the last 20 years (Fig. 7), YFT genetic population structure remains poorly understood. Studies have used different samples and genetic markers that have led to discordant intra- or inter-oceanic patterns of differentiation (Table 3). The first attempt to delineate YFT stock structure was completed more than 50 years ago (Suzuki 1962). This study used
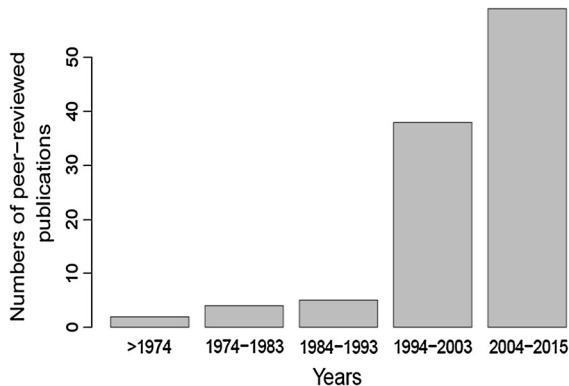
Fig. 7 Number of peer reviewed articles about the genetic population structures of tuna and tuna like species published since the 1960s. *Source*: *Web of Science* and *Science Direct*

immunological markers as the transglutaminase blood antigens to discriminate between PO and IO stocks. Although this study failed to achieve its broader goal, it did demonstrate the unsuitability of this method. A variation analysis of enzyme electrophoretic mobility (i.e., allozyme analysis) was used by Sharp (1978) to detect significant genetic differentiation between WCPO and EPO YFT samples at the glucose-phosphate isomerase (GPI) locus. This result was corroborated by Ward et al. (1994) who detected significant heterogeneity at the GPI-F* allozyme locus. Their results were, however, contradicted by the lack of genetic divergence in the mtDNA restric-tion fragment length polymorphisms (mtDNA-RFLP) observed in samples from the same areas (Scoles and Graves 1993; Ward et al. 1994). The lack of mtDNA-RFLP differentiation could be due to the small sample size (five locations in the PO and a single location in the AO), or the very small number of restriction enzymes employed (*BclI* and *EcoRI*) that prevented sufficient genetic variation from being detected at the nucleotide level. Later, using allozyme and mtDNA-RFLP marker analyses, Ward et al. (1997) suggested the existence of four distinct YFT genetic populations in the AO, IO, WCPO and EPO. In contrast, later

Table 3 A comparison of the results of yellowfin tuna (*Thunnus albacares*) genetic population studies using tradi tional molecular markers [allozymes (1); mtDNA (2); microsatellites (3); and other (4)] between and within the four tuna Regional Fisheries Management Organizations (tRFMOs) where x denotes a significant difference, denotes no difference and ^ means not analyzed

Source	Method 1	Method 2	Between RFMOs	Within RFMOs
Suzuki (1962)	4			
Sharp (1978)	1		x	
Scoles and Graves (1993)	2			
Ward et al. (1994)	1	2	x	
Ward et al. (1997)	1	2	x	
Chow et al. (IOTC 2000)	2			
Nishida et al. (IOTC 2001)	4		^	
Appleyard et al. (2001)	3			
Ely et al. (2005)	2			
Díaz Jaimes And Uribe Alcocer (2006)	3		^	x
Dammannagoda et al. (2008)	2		^	x
Wu et al. (2010)	2			
Kunal et al. (2013)	2		^	x
Li et al. (2015)	2		^	x
Aguila et al. (2015)	3		^	x
Pecoraro (2016)	3			

studies that used different markers (i.e., microsatellites, mtDNA sequences and PCR RFLP profiles) suggested that YFT have a single large panmictic population that covers the four different oceans (Appleyard et al. 2001; Chow et al. 2000; Nishida et al. 2001; Ely et al. 2005; Wu et al. 2010). These studies suggested that the Cape of Good Hope may not represent a geographical barrier to YFT gene flow although it does for BET (Alvarado Bremer et al. 1998; Martínez et al. 2006; Chiang et al. 2008) and billfish species (blue marlin: Finnerty and Block 1992; Graves and McDowell 1995; swordfish: Alvarado Bremer et al. 1996; Chow et al. 1997; Chow and Takeyama 2000; sailfish: Graves and McDowell 1995). This reduced genetic differentiation among YFT populations, as compared to those detected for other tuna and tuna-like species, is probably linked to the larger population size of YFT and its association with higher levels of standing genetic variation (Ward et al. 1994; Ely et al. 2005). This hypothesis has been supported by the survey we carried out on five geographical samples (N = 163), employing six microsatellite loci recently isolated for YFT (Antoni et al. 2014) and six microsatellite loci isolated for southern bluefin tuna, *Thunnus maccoyii* (P. Grewe, pers. com.). Our results showed very low levels of spatial genetic differentiation that were not significant, within or between the AO, IO, EPO and WCPO (Table 4; Pecoraro 2016).

In contrast, a few recent studies completed for the IO and PO have looked at YFT population structure at a much smaller scale than previously considered for stock assessments and management strategies (Díaz-Jaimes and Uribe-Alcocer 2006; Dammannagoda et al. 2008; Kunal et al. 2013; Aguila et al. 2015; Li et al. 2015). The analysis of seven simple sequence repeat loci showed significant differentiation between

YFT in the northern and southern regions of the EPO ($F_{CT} = 0.016$; $P = 0.011$) but no significant differences ($F_{SC} = 0.0017$; $P = 0.315$), within samples taken from the same area (Díaz-Jaimes and Uribe-Alcocer 2006). These results are consistent with those obtained from tagging studies in the north EPO and collectively support the assumption that YFT display site fidelity (Schaefer et al. 2007, 2011). The possible existence of different sub-populations has also been detected within the central PO using the mtDNA COI gene sequences (Li et al. 2015), and between the central and western regions of the PO, using ten microsatellite loci (Aguila et al. 2015). Significant genetic differentiation has also been revealed among sites in the north-western IO, using both the mitochondrial ATPase 6 and 8 regions (498 bp) and two microsatellite loci (Dammannagoda et al. 2008). The hypothesis that different sub-populations are present in the northern IO was corroborated by Kunal et al. (2013) who detected at least three different genetic populations in IO waters by analyzing the sequence of mtDNA D-loops. The presence of these different populations may also be explained by fidelity to different spawning areas within the IO. In this area, the main spawning ground lies west of 75°E, with secondary spawning areas found off Sri Lanka, in the Mozambique Channel and off eastern Australia (IOTC 2015). The high degree of differentiation observed at these smaller geographical scales has also raised many doubts about the actual YFT population structure. As population structure has wide-ranging implications for management, these doubts highlight the necessity of investigating this issue in more depth, both within and between oceans. In this context, access to more powerful and cost effective genetic and genomic tools (e.g., next generation sequencing technologies; NGS) would represent a clear way forward for resolving the stock structure of YFT at differing scales.

Switching from YFT genetics to genomics

The previous section implies a central question, "Why are there apparent conflicting genetic patterns in YFT at both local and global scales?". The most logical answer is that YFT display both high fecundity and large population sizes that make it difficult to detect genetic differentiation among population samples (Ely et al. 2005; Juan-Jordá et al. 2013a; Pecoraro et al.

Table 4 Pairwise F_{ST} values calculated among yellowfin tuna samples (from the Atlantic, Indian and Pacific Ocean) are reported (below the diagonal) with their associated *P* values (above the diagonal)

	WCPO	EPO	EAO	WAO	WIO
WCPO	*	0.46233	0.3166	0.28868	0.63796
EPO	0.00066	*	0.61865	0.51926	0.53915
EAO	0.00134	0.00038	*	0.90971	0.3173
WAO	0.00107	0.00024	0.00302	*	0.04574
WIO	0.00032	0.00012	0.00111	0.00372	*

2016). These characteristics, together with the fact that genetic studies to date have focused on a relatively small number of molecular markers distributed in a limited portion of the genome (Appleyard et al. 2001; Díaz-Jaimes and Uribe-Alcocer 2006), have led to results that are not suitable for determining the stock structuring used by the tRFMOs (Pecoraro et al. 2016). These limitations are further underlined by the fact that genes are not islands but rather, part of a genomic community bound by both physical closeness on chromosomes and by various evolutionary processes (Bonin 2008). In this context, the advent of NGS technologies and the consequent decrease in high-throughput sequencing costs have opened up new possibilities for the identification of thousands of co-dominant single nucleotide polymorphisms (SNPs) at a genome-wide scale (Davey et al. 2011). This will increase the power of genetics to discriminate weakly differentiated YFT populations (Grewe et al. 2015; Pecoraro et al. 2016). NGS approaches provide a better representation of the genome, allowing the disentan-gling between neutral evolutionary processes (i.e., genetic drift) and those influenced by selection (e.g., local adaptation which translate into differentiated local populations). The application of genome-wide scan approaches to detect potential signatures of local adaptation in non-model organisms has been enabled by NGS. Current methods allow the identification of outlier loci which show higher genetic divergence among natural populations than expected under neutral conditions, thus responsible for potentially adaptive population divergence. There is, therefore, an urgent need to switch from genetics to genomics to better define proper biological and consequently management units in highly migratory species (Grewe et al. 2015). The need to adopt a genome-wide perspective for disentangling the YFT population structure is corroborated by SNP markers evidence, which shows that genetically distinct populations are present at the ocean basin scale (Grewe et al. 2015; Pecoraro et al. 2016). An early illustration of the efficiency of SNPs in assessing genetic divergence in marine fish with high dispersal potential, was highlighted by Pecoraro et al.(2016). In this study, the 2b-RAD genotyping tech-nique (Wang et al. 2012) was used to investigate the YFT population structure between the AO, IO and PO ($F_{ST} = 0.0273$; P value <0.01).

Grewe et al. (2015) confirmed the presence of two distinct populations in the EPO and WCPO. However, after discovering a panel of 18 SNPs considered to be under positive selection, two distinct sub-populations were determined to exist in the Coral Sea and around Tokelau, both of which occur within the WCPO. These results demonstrate the potential of genomic approaches for detecting the population structures of highly migratory pelagic species, but also highlight the need to have a representative sampling, especially at local scales. They also suggest that the way YFT conservation units are assessed and managed in the PO may need to be redefined (Grewe et al. 2015), even if inter-annual stability of the genetic structure needs to be verified. Grewe et al. (2015) also demonstrate the need to carry out finer scale population structure studies, using selected panels of outlier loci presumed to be under divergent selection. In fact, for species with high migration rates and large population sizes, simply increasing the number of neutral markers may not be enough to reveal population connectivity, especially at the local scale (Gagnaire et al. 2015; Hauser and Carvalho 2008).

Sampling strategies and the misidentification issue between juveniles

Discrepancies in the genetic results obtained for YFT may also be due to sampling design. In order to properly identify management units for such a highly migratory species, an intensive sampling effort should be performed to enable a comprehensive assessment of the population structure. The first key factor to take into consideration is sample size (Viñas et al. 2011). Typically, a sample size of 50 individuals is consid-ered adequate for population genetic studies so as to limit the sampling noise when estimating the genetic distance among samples (Nei 1987). For example, sampling too few individuals that are close relatives has been shown to result in the overestimation of population divergence and led to the misinterpretation of meaningful structural components (Allendorf and Phelps 1981; Waples 1998). Since YFT are capable of performing long distance migrations (Block and Stevens 2001), a sampling effort that only focused on adults or sub-adults in a specific area might lead to the selection of a group that originated from different spawning areas and any possible differences in genetic signatures would be confused. In contrast, the collec-tion of larvae and individuals considered to be the young of the year (i.e., post-larval and early-stage

juveniles), life stages that are characterized by a limited swimming ability, will better reflect the true genetic composition of the spawning populations (Carlsson et al. 2007), as such individuals are assumed to be caught close to their spawning areas. The post-larval and early-stage juveniles of many tuna and tuna-like species are, however, morphologically similar, especially within the same genus (Robertson et al. 2007), and accurate identification requires advanced taxonomic skills. If individuals have been frozen or exposed to other processes (e.g., canning, filleting), the use of morphological characters (i.e., body shape, pigments, fin characteristics, etc.) are deceptive, making accurate identification impossible. This is particularly true for small-sized YFT and BET, whose morphological differences below a certain size (<30 cm F_L) are almost imperceptible (Itano 2005). It is essential, however, that we discriminate between juveniles of these two species to obtain more accurate data about recruitment, population structure, and spawning seasons and areas. Consequently, different protocols based on molecular markers may help, but due to the short evolutionary distance between both species, the results of these analyses can be confounded if a marker with low genetic variability is used. To properly discriminate the two species, the mtDNA control region can be a robust marker when used in association with a liver morphology test (Pedrosa-Gerasmio et al. 2012), as has the nuclear genetic marker ITS1 (first internal transcribed spacer of the nuclear rDNA genes; Viñas and Tudela 2009). The ATCO gene region, which is the flanking region between the ATPase and cytochrome oxidase subunit III genes (Chow and Inoue 1993), was also verified as one of the highest performing markers in discriminating between these two species. Michelini et al. (2007) also demonstrated the utility of a multiplex-based polymerase chain reaction as a rapid molecular instrument for this task. In addition, it may also be desirable to carry out multi-annual sampling in order to temporally replicate efforts in the same areas, with a view to identifying true stock boundaries.

Conclusions and YFT future research directions

Because YFT are a multi-billion dollar common resource, with ever increasing fishing pressure, there is a growing need to advance our understanding of its stock structure to ensure proper and sustainable management. Our review indicates that YFT management is not currently matched to the biological structure outlined by tagging and genetic studies, that indicate the presence of populations more structured than typically assumed. Tagging results have showed an high site fidelity of the recovered YFT to their tagging position, suggesting that various fractions of YFT stocks are not randomly traveling across their potential habitat (Fonteneau and Hallier 2015). Those individuals seem to have the capability to remember their exact natal location, where they come back for spawning (i.e., Gulf of Guinea; Zagaglia et al. 2004). Due to the limited genetic resolution of classical markers and the large-scale movements of this species that would probably provide a low genetic exchange rate, genetic results have provided different information from tagging results, obscuring evidences of global population structure (Ely et al. 2005; Pecoraro et al. 2016). There is, therefore, a need to establish more accurate and realistic population boundaries, incorporating independent, multi-approach fisheries data, such as those from population genomics and chemical tags in otoliths. Considering different sub-populations as a unique panmictic population will increase the risk of mismanagement. Consequently, failure to achieve current conservation and sustainable use objectives is likely, especially in areas where there is a current mismatch between management units and true population structure (i.e., EPO and WCPO). Genomic tools may be very useful to resolve the population structure of YFT, both spatially and temporally, within separated spawning grounds and areas where populations are mixed. These tools offer a way to screen large sets of neutral genetic markers at the genome-wide scale, improving our ability to estimate the effects of demographic processes and the effective population size (Ne), using both temporal or single-sample estimators (Palstra and Fraser 2012) that determine the genetic properties of a population (Hauser et al. 2002). The Ne plays a central role in defining how demographically, environmentally or genetically stochastic events can affect a species persistence and fitness (Palstra and Fraser 2012). In marine fishes, this is particularly true because Ne is generally much lower than the adult census size (N) in natural populations (Palstra and Ruzzante 2008). Populations of millions of individual fish may be dependent on a Ne of only several hundreds or

thousands of individuals (Hauser et al. 2002). Despite the importance of this parameter, it has never been estimated for YFT populations. This parameter would increase our understanding as fishery and environmental changes are influencing genetic diversity, enabling us to forecast possible short- and long-term evolutionary scenarios. The genomic approach represents the life-blood for the conservation of this species, facilitating the increased precision and accuracy of *Ne* estimates, sound management and the genotyping of hundreds to thousands of neutral loci in numerous individuals. Consequently, a casualness of these information would represent a loss of an important perspective in our attempt to match assessment with true biological boundaries.

Further, genomic approaches may also increase statistical power, meaning that we are able to detect finer levels in population structures through the identification of outlier loci at the genome scale, presenting new opportunities to detect the genetic basis of local adaptation. Given the high degree of uncertainty that still surrounds our understanding of the population structure of YFT, such knowledge would greatly improve the management of YFT populations at the global scale.

We also note the importance of including other key biological parameters into the YFT stock assessments, facilitating the development of more realistic population dynamics models and effective fisheries management strategies. For instance, YFT stock productivity should take into account a variety of fundamental attributes, such as the onset of maturity, fecundity, atresia, the duration of the reproductive season, daily spawning behavior and the spawning fraction (Murua et al. 2003). If productivity is only measured on the basis of spawning biomass estimates, the risk is that productivity (and the stock's inherent ability to deal with pressures from fisheries and environmental changes) will be overestimated. This is because spawning biomass estimates are currently based on the assumption that fecundity is correlated with mass-at-age values obtained from the sexually mature portion of the population, irrespective of the demographic composition of adults (Murawski et al. 2001; Kell et al. 2015). Future efforts need to focus on evaluating the reproductive importance of large and experienced spawners in order to properly estimate the true reproductive potential of YFT. Such analyses may prove essential for rebuilding the stock. In addition,

the evident sexual-dimorphism in growth must also be considered in YFT stock assessments. This is just one of the current limitations of the statistical models used in the stock assessments of all four ocean basins. Although these models try to account for changes in natural mortality by considering age, sex, movements and migrations, these aspects are all considered to be fixed in time. This oversimplifies the spatio-temporal variability of oceanographic features that drive YFT distribution. There is a strong relationship between physical and biological environment conditions, YFT physiological abilities and tolerances, and YFT population dynamics and distribution (Horodysky et al. 2016). This relationship makes necessary to develop ecosystem-based approaches to integrate these variations into the stock assessment models. In addition, these models should take into account the spatially-distributed effects of fisheries on the modeled population to investigate the impacts of both fishing and environmental variability (Lehodey et al. 2008). The behavior of YFT to associate with floating objects should be further studied and modeled, as fisheries employing FADs are becoming continually more common (Maufroy et al. 2016). The great advantage of using ecosystem-based models lies in their potential to avoid trivializing the complex mechanisms that drive the spatio-temporal fluctuations and dynamics of YFT populations, but rather, account for variability over long time scales (e.g., the impacts of global warming; Lehodey et al. 2011).

Progress also needs to be made in improving data collection, adaption of reference points and development of HCRs. HCRs should consider the relevant aspects of biology, ecology, stock structure and fisheries status underlined in this review. Currently, reporting of tuna fisheries data to the tRFMOs by most coastal nations is poor due to a lack of capacity and funding and, in some instances, political reasons. In particular, the misidentification of small YFT in various fisheries (e.g., gill nets) can strongly bias the catch-at-size data that are subsequently used as inputs for the stock assessment models. In the near future, more effort should be also directed to improve the interactions and the dialogue between researchers, stakeholders and policy makers, specifically in regards to setting out stock-specific limits, target reference points and strategies to avoid overfishing and to rebuild depleted stocks. This is particularly important because improvements in scientific research alone are

not enough to secure improvements in the long term management and sustainability of YFT.

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