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A review of the fisheries, life history and stock structure of tropical tuna (skipjack *Katsuwonus pelamis*, yellowfin *Thunnus albacares* and bigeye *Thunnus obesus*) in the Indian Ocean

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Abstract :

Skipjack (Katsuwonus pelamis), yellowfin (Thunnus albacares) and bigeye (Thunnus obesus) tuna are the target species of tropical tuna fisheries in the Indian Ocean, with high commercial value in the international market. High fishing pressure over the past three decades has raised concerns about their sustainability. Understanding life history strategies and stock structure is essential to determine species resilience and how they might respond to exploitation. Here we provide a comprehensive review of available knowledge on the biology, ecology, and stock structure of tropical tuna species in the Indian Ocean. We describe the characteristics of Indian Ocean tropical tuna fisheries and synthesize skipjack, yellowfin, and bigeye tuna key life history attributes such as biogeography, trophic ecology, growth, and reproductive biology. In addition, we evaluate the available literature about their stock structure using different approaches such as analysis of fisheries data, genetic markers, otolith microchemistry and tagging, among others. Based on this review, we conclude that there is a clear lack of ocean basin-scale studies on skipjack, yellowfin and bigeye tuna life history, and that regional stock structure studies indicate that the panmictic population assumption of these stocks should be investigated further. Finally, we identify specific knowledge gaps that should be addressed with priority to ensure a sustainable and effective management of these species.

Keywords : Indian Ocean, Tropical tuna, Fisheries, Life history, Stock structure, Tuna biology, Tuna ecology, Skipjack tuna, Yellowfin tuna, Bigeye tuna

1. Introduction

Skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) tuna are members of the Scombridae family. They are commonly referred to as tropical tuna because they inhabit tropical and subtropical waters of the three major oceans (Atlantic, Indian, and Pacific). These species represent a vital source of food, employment and livelihood for numerous coastal communities and nations (FAO, 2016). Two main markets drive tuna production; traditional canned tuna, dominated by light meat species such as skipjack and yellowfin, and sashimi/sushi products, where red meat species such as bluefin and bigeye tuna are preferred (FAO, 2018). Market demand for tuna has increased over the last few decades, which has led to increased exploitation. Global catch of tuna species in 2018 was 5.1 million tonnes, of which tropical tuna species accounted for 95% (ISSF, 2020). In addition to being a major component of the global fishing industry, tropical tuna are also amongst the world´s most valuable fish (Galland et al., 2016), Tropical tuna contribute considerably to the global economy ($29.17 billion market value), and account for the 88.5% of the global tuna sales value in 2014 (Macfadyen, 2016). The Pacific Ocean supports the world´s largest tuna fisheries, followed by the Indian Ocean, which accounts for 21% of worldwide tropical tuna catches (Galland et al., 2016). Tropical tuna are an important source of food for millions of people around the world, and support the livelihoods and employment of local communities and fishermen who depend on them (FAO, 2016). These species are top predators that play a significant role in the open ocean ecosystems, due to their influence in marine food webs structure and dynamics (Estes et al., 2016; van Denderen et al., 2018), hence their decline can initiate trophic cascades (Heithaus et al., 2008), and jeopardise the resilience and stability of marine resources (Kerr et al., 2016).

Despite their inherent importance to the marine ecosystem, the global economy and human wellbeing, the complex and diverse range of countries participating in tuna Regional Fisheries Management Organizations (tRFMOs), organizations responsible for managing tuna and tuna-like species, hinder the implementation of effective conservation strategies to ensure the sustainability of tuna and related ecosystems (Cullis-Suzuki and Pauly, 2010; Collette, 2017; Juan-Jordá et al., 2017). This is particularly true in the Indian Ocean, where the co-existence of artisanal and industrial fisheries (total catches are divided about equally between them), poses a major challenge for the assessment and management of Indian Ocean tropical tuna stocks by the Indian Ocean Tuna Commission (IOTC) (Murua et al., 2015; McCluney et al., 2019). Overall, data collection is less coordinated and naturally more difficult when it comes to small vessels, and management and enforcement outcomes harder to implement (Pons et al., 2017). Many developing countries experience serious capacity and infrastructure constraints, which can impede adequate data collection and reporting (Ceo et al., 2012). And this is particularly the case of the Indian Ocean, where for many tuna species artisanal fisheries, and in some case semi-industrial, tuna catches are estimated by IOTC using several sources of information (see for more details IOTC, 2019c). The difficulty of monitoring the fisheries within the Indian Ocean not only affects the stock assessment process, but also the implementation of the agreed management measures in the IOTC area. For instance, although catch limitations of yellowfin tuna in the Indian Ocean were agreed due to the overfished status of the stock (IOTC Resolution 19/01), the measure failed to achieve its goal as catches has increased by around 9% in 2018 from 2014/2015 levels despite limitations (IOTC, 2019b). Similarly, a Harvest Control Rule was agreed in 2016 for skipjack tuna (IOTC Resolution 16/01), but the resultant catch limit for 2018-2020 has been exceeded in 2018 (IOTC, 2019b). As mis-assessment and mis-management of a species can lead to stock depletion (Hutchings, 2000; Pauly et al., 2003), efforts must focus on improving the capacity of monitoring the fishery to collect fishery statistics and statistical methods needed for improved assessment as well as improving the capacity to implement the agreed management measures of the three tropical tuna stocks (i.e., skipjack, yellowfin and bigeye) under the IOTC mandate.

Understanding life history strategies and stock structure is essential in determining how a species might respond to fishing pressure (Jennings et al., 1998; Begg et al., 1999; Juan-Jordá et al., 2013). Life history information such as age and growth, reproduction, maturity and mortality is required to determine population productivity and, hence, resilience to fisheries (King and McFarlane, 2003; Morgan et al., 2009), while the knowledge on habitat utilization and niche exploitation at different life stages can be useful for evaluations of species-specific vulnerability to different fisheries. Besides, the understanding of stock structure helps determine the appropriate units for stock assessment and suitable spatial scale for management (Kerr et al., 2016). Different stocks (i.e. semi-discrete groups of fish with some definable attributes that are of interest to fishery managers *sensu* Begg and Waldman 1999) may possess specific genetic, physiological or/and behavioral traits, that can influence life history processes (Stepien, 1995). As such, when the stock structure is more complex than recognized, management measures based on a single stock assumption can potentially lead to overexploitation and possible collapse of less productive subpopulations, and under-exploitation of more productive populations (Stephenson, 1999; Ying et al., 2011). Each tropical tuna species is considered to form a single stock in the Indian Ocean for management purposes (IOTC, 2017a, 2017b, 2017c) although spatial structure is recognized in current stock assessments, which need to determine relative abundances among regions (Hoyle, 2018; Hoyle and Langley, 2020). Since 2008, Indian Ocean yellowfin tuna assessments used a spatial stratification (Langley et al., 2008; Fu et al., 2018), and so did recent bigeye assessments (Langley, 2016; Fu, 2019). These models consider spatial differences in catches but assume a single-stock recruitment relationship (i.e. a unique spawning population with no reproductively isolated units). However, scientific evidence on how tropical tuna are structured in the Indian Ocean is required to validate the adequacy of the divisions used in this approach and to resolve the single stock hypothesis assumption, as different scenarios may lead to different management strategies and implications (Fig.1)

The aim of this review is to (i) describe the particularities of Indian Ocean tropical tuna fisheries (ii) synthesize the existing information on Indian Ocean skipjack, yellowfin and bigeye tuna life history strategies, (iii) compile the available information on stock structure sourced from studies using a range of different approaches, and (iv) identify major knowledge gaps and highlight future research priorities needed for the implementation of an effective conservation strategy for the tropical tunas in the Indian Ocean.

2. Tropical tuna fisheries in the Indian Ocean

Tropical tunas are the main target species of many industrial and artisanal fisheries in the Indian Ocean, representing 53% of the total IOTC catches in 2018. Of the tropical tunas, skipjack tuna contributes the most to catches (~53%), followed by yellowfin (~38%) and bigeye (~9%) tuna (IOTC, 2019a). Tuna fishing operations increased rapidly during the 1980s (Majkowski et al., 2011; Marsac et al., 2014), with tropical tuna catches growing from 146,483 tonnes (t) in 1980 to 560,308 t in 1990. At the beginning of the 20th century, catches reached record levels, with 1,204,041 t reported in 2005. Over the last decade, total catches have fluctuated between ~0.8-1.0 million tonnes, with evidence of an increasing trend since 2015 with 1,130,359 t landed in 2018 (IOTC, 2019a) (Fig. 2a). Until the late 1960s catches of tropical tuna were dominated by Japan, but the large increase of catches during the 1980s was mainly driven by Taiwan, European Union, Maldives and Indonesia (Fonteneau, 2010).

A characteristic of the Indian Ocean tropical tuna fishery is the relatively high contribution by the artisanal sector (e.g., handline, gillnet, and pole-and-line) with around of 50% of total Indian Ocean tuna catches. Domestic fisheries represent the main livelihood for millions of people in developing countries of the eastern African coastal countries (van der Elst et al., 2005; Walmsley et al., 2006), and are of crucial importance for food and employment security (Christ et al., 2020). At the beginning of the 2000s, these fisheries accounted for ~35% of the total catch, exceeding 50% in the 2010-2014 period, after which it steadily decreased down to ~43% in 2018 (Fig. 2b). The remaining catch is landed by industrial purse seiners and longliners (Murua et al., 2015; IOTC, 2019a). The contribution of each fishing gear to the catch varies among species. During the 2014-2018 period, skipjack tuna was mostly caught by industrial purse seiners (~40%), pole-and-line (~20%), and gillnet (~20%) whereas yellowfin was mostly caught by purse seiners (~36%), handline (~29%,) gillnet (~21%) and longline (~10%) (IOTC, 2019b). This indicates, that for these two species, catches are relatively evenly split between industrial and artisanal fisheries. By contrast, industrial fisheries account for the majority of bigeye tuna catches in the Indian Ocean; deep-freezing and fresh longline (~42%) and purse seiners (~31%) for the 2014-2018 period (IOTC, 2019a).

The majority of tropical tuna catches in the Indian Ocean are taken from the western region, with ~80% of total catches occurring west of 80ºE (i.e. FAO fishing area 51) in 2018 (IOTC, 2019a). However, location of catches can vary seasonally, interannually and between gear types (Kaplan et al., 2014). Longline fisheries operate throughout the entire Indian Ocean but catches of tropical tunas (primarily bigeye and yellowfin tuna) are predominantly taken between latitudes 30°S-20°N, and peak from November to June (Fig.3). From November to February (Fig. 3a), high catches are widespread from west to east whilst they become concentrated in the Somali basin, north of 5°S, from March to June (Fig. 3b). Although catches in July to October are generally lower than other months, they are again spread across the whole ocean basin (Fig. 3c). An interesting characteristic of the fishery is the dominance of yellowfin tuna in catches in the Mozambique Channel and the Bay of Bengal, in all seasons, whereas bigeye is the primary target species in the equatorial region of the fishery. To a lesser extent, longline fisheries also operate in the southern Indian Ocean along a zonal region between South Africa and Australia, where bigeye (and albacore – not shown here) is caught as a bycatch of the southern bluefin fishery.

Purse seiners fishing activity is mainly concentrated in the western and central Indian Ocean, between latitudes 20°S-15°N (Fig.4). Skipjack tuna, and to lesser extent juveniles of yellowfin and bigeye tunas, are the predominant species caught by purse seiners fishing around fish aggregating devices (FADs) (Fig.4a, c and e), while yellowfin tuna dominate catches by purse seiners fishing on free-swimming schools (Fig.4b, d and f). From November to February, purse-seine catches on FADs are mainly in the western-equatorial Indian Ocean (Fig.4a), whereas purse seine catches on free-swimming schools increase around the Seychelles and Chagos archipelagos (Fig.4b). From March to June, the purse seine fishery operates in the western-equatorial area but extends as far south as the Mozambique Channel, which is a mixture of FAD and free school fishing (Fig.4c and d). During this period, tropical tuna catches by purse seiners are also higher off the East African continent relative to central Indian Ocean. During the southwest monsoon (July-October, Fig.4e and f), catches shift northward 5ºS again, being highest off Somalian coast up to the Seychelles archipelago.

Spatio-temporal patterns of activity of artisanal and semi-commercial fisheries cannot be described accurately because spatialized catch and effort data are not usually provided by the fleets. Within the Indian Ocean, the major pole-and-line fishery occurs in Maldives. This fishery is active all year round, targeting mainly skipjack tuna, and to less extent yellowfin tuna (Kolody and Adam, 2011; Miller et al., 2017). Maldivian hand-line also operates year around catching large yellowfin (Ahusan et al., 2016). The gillnet fishery of yellowfin tuna is also important in Sri Lanka, Pakistan and Iran, catching yellowfin and skipjack (IOTC, 2019b).

Since 2001 a significant progress has been made to reduce illegal, unreported, and unregulated fishing (IUU) within the Indian Ocean (Anganuzzi, 2004; Agnew et al., 2009), but the true extent of this problem may be underestimated due to paucity of information on non-industrial fisheries (Pauly and Zeller, 2016). Considering all fisheries in the region (not only tuna), reconstructed catch trajectories of the Indian Ocean differ considerably from the national landings data submitted to the FAO, especially in the western region (Pauly and Zeller, 2016). Inconsistencies between reported landings and reconstructed catch data for all taxa have been described for the south-western Indian Ocean (Temple et al., 2018), the Seychelles (Christ et al., 2020), Madagascar (Le Manach et al., 2016) and Somalia (Glaser et al., 2019).

3. Life history

Skipjack, yellowfin and bigeye tuna are classified into the Scombridae family, and together with the other 12 tuna, form the tribe Thunnini. Among the five genera that form this tribe, yellowfin and bigeye tuna belong to the genus *Thunnus* while skipjack tuna belongs to the genus *Katsuwonus* (Collette et al., 2001) (Fig. 5). Tunas (except *Allothunnus sp.*) are unique among bony fishes as they possess a counter-current heat exchanger system of *retia mirabilia* (i.e., a vein-arterial vascular system for heat conservation in muscles, viscera and brain tissue) that allows them to maintain the temperature of body tissue warmer than the surrounding waters (Collette et al., 2001). This endothermy, along with an elevated metabolic rate and frequency modulated cardiac output, support continuous, relatively fast swimming and reduce thermal barriers to habitat exploitation (Graham and Dickson, 2004). Skipjack and yellowfin tuna possess both central and lateral heat exchangers, although lateral retia mirabilia are relatively small. Bigeye tuna have no central heat exchanger, but a well-developed lateral heat exchanger (Carey et al., 1971; Graham, 1975), as well as an additional retia, the function of which is to increase the temperature of their viscera, eyes and brain. This allows bigeye to explore deeper and cooler waters than yellowfin or skipjack. These adaptations imply different life history traits and behaviours among the three species of tropical tuna (Díaz-Arce et al., 2016).

3.1. Biogeography and habitat utilization

Tropical tuna are circumtropical species that inhabit marine pelagic regions of the world's oceans between 45ºN and 45ºS (Fig. 6) (Sharp, 2001). Whereas adult yellowfin and bigeye tuna inhabit mid-ocean waters, juveniles of these species and skipjack tuna can be found both in coastal and offshore waters (Goujon and Majkowski, 2010). In the Indian Ocean, the three species are more abundant between the 15ºS-15ºN longitudinal band, the Arabian Sea and the Mozambique Channel, although they can also be found in other regions (Stéquert and Marsac, 1989; Lee et al., 2005; Kaplan et al., 2014). North of 10ºS, the Indian Ocean is characterized by a marked seasonality, due to the monsoonal system that determines the ocean circulation and climate (Schott and McCreary, 2001). Two monsoon periods occur annually, the southwest monsoon (June-September) and the northeast monsoon (December-March), with two inter-monsoon periods in between, one from April to May and the second from October to November (Schott et al., 2009; Han et al., 2014). In addition, there is a non-periodical mode of natural climate variability in the Indian Ocean, known as the Indian Ocean Dipole (IOD). This phenomenon is the result of sustained changes in the differences between sea surface temperatures (SST) of the western and eastern Indian Ocean (Saji et al., 1999). Both processes have an impact on the biological production and ecological processes of the area (Wiggert et al., 2006; Jury et al., 2010), and thus may affect the seasonal distribution and behaviour of tropical tuna in the Indian Ocean (Marsac and Le Blanc, 1998, 1999; Ménard et al., 2007b; Marsac., 2017).

Although investigations of Indian Ocean tuna habitat preferences are scarce, experimental studies (Dizon et al., 1977; Sharp and Dizon, 1978; Sharp, 2001) have defined the main environmental preferences and physiological adaptation characterizing tuna habitats. As confirmed by other authors (e.g. Reygondeau et al., 2012; Arrizabalaga et al., 2015; Druon et al., 2017), tropical tuna prefer relatively warm and stratified waters. Skipjack, yellowfin and juvenile bigeye tuna inhabit the epipelagic zone, preferentially occupying the surface mixed layer above the thermocline and waters with sea surface temperatures (SSTs) ranging from 18 to 31°C (Barkley et al., 1978; Stéquert and Marsac, 1989; Pecoraro et al., 2016). Particularly in the Indian Ocean, adult yellowfin tuna preferred habitat has been described to be at depths between 100 and 180m and water temperatures between 15.0-17.9°C (Song et al., 2008). By contrast, adult bigeye tuna inhabit mesopelagic waters, and prefer depth and water temperatures between 240 and 280 m and 12 to 13.9°C, respectively (Song et al., 2009).

Tropical tuna larvae require warmer water (Conand and Richards, 1982; Wexler et al., 2011; Kim et al., 2015), being confined to narrower habitat ranges than juveniles and adults (Reglero et al., 2014) (Fig. 6). The isothermal boundary of tropical tuna spawning areas is >24°C (Schaefer, 2001), although Reglero et al., (2014) suggested that this assumption should be revisited as they found a lower tolerance for tropical tuna larvae of 20°C. Larval occurrence seems to increase at intermediate values (0.01-0.06 $m^2 s^{-2}$) of eddy kinetic energy (Kimura et al., 2004; Reglero et al., 2014).

Despite temperature preferences restricting tropical tuna spatial distribution, electronic tagging has shown that these species are able to perform deep dives into colder waters (e.g. Schaefer et al., 2009). Depth preference is known to change according to body size (Barkley et al., 1978; Graham and Dickson, 2004) and time of the day (Evans et al., 2008). In the Indian Ocean, deep diving behaviour has only been studied in yellowfin tuna; archival tagging of adults showed that large individuals can dive to depths in excess of 1000 m (Dagorn et al., 2006). Oxygen availability also limits the bathymetric range of tropical tuna species. Skipjack and yellowfin tuna have limited tolerance to low levels of dissolved oxygen (Barkley et al., 1978; Graham and Dickson, 2004), while bigeye tuna can tolerate, and even favour, less oxygenated (e.g. <0.2 mmol/L) waters (Sharp and Dizon, 1978; Graham and Dickson, 2004; Song et al., 2009; Arrizabalaga et al., 2015). These species-specific physiological abilities and tolerances to environmental characteristics of their vertical habitat, result in exploitation of distinct ecological niches at different stages of their life-histories.

3.2. Trophic Ecology

Tropical tuna have been described as energy speculators, meaning that high rates of energy expenditure are invested to obtain even higher rates of energy (Korsmeyer and Dewar, 2001). Thus, their lifestyle implies the necessity for searching large areas of their habitat in search of food (Dickson, 1995). As such, tropical tunas are visual opportunistic predators that feed on a wide variety of prey (Olson et al., 2016; Duffy et al., 2017); the particular composition will be mainly determined by body size, location, period and feeding depth of each species (Ménard et al., 2006; Olson et al., 2016). In the Indian Ocean, studies analyzing the composition and size of the prey in stomachs of skipjack, yellowfin and bigeye tuna, are limited to the western region.

As larvae and small juveniles, tropical tuna diet consists of planktonic organisms inhabiting the shallow mixed layer (Young and Davis, 1990; Graham et al., 2007). Tuna larvae are precocious feeders; skipjack larvae start feeding two days after hatching (Matsumoto et al., 1984), while rotifers have been found in digestive tracks of 4-day old yellowfin tuna larvae (Kaji et al., 1999). With the development of thermal capability, a progressive diet shift occurs (Kaji et al., 1999; Graham et al., 2007). Maldeniya (1996) found a gradual increase in fish consumption in yellowfin tuna > 40 cm fork length (FL) from Sri Lanka. This ontogenetic shift in diet has also been reported for bigeye tuna of the Indian Ocean: the diet of juvenile bigeye tuna consists mainly on stomatopod crustaceans, while piscivory increases in larger specimens (Duffy et al., 2017). Juveniles of skipjack, yellowfin and bigeye tuna can be found in mixed schools feeding at the surface, generally near the continental shelf, islands or around floating objects (IOTC, 2017a, 2017b, 2017c). Trophic markers revealed high potential of resource overlap between smaller individuals of these species (Sardenne et al., 2016).

In contrast, adults consume a larger range of prey sizes (mainly small fish, cephalopods and crustaceans) (Ménard et al., 2007a; Jaquemet et al., 2011; Olson et al., 2016), and exhibit predation plasticity depending on prey availability between times and locations (Olson et al., 2016; Duffy et al., 2017). Changes in diet composition with distance from the coast have been reported for skipjack and yellowfin tuna (Smale, 1986). Small pelagic fish (*Cubiceps pauciradiatus*, *Sardinella ocellata* and *Engraulis capensis*) dominate by volume for skipjack and yellowfin tuna diets near the shore (Smale, 1986; Potier et al., 2008), whereas in open-ocean waters the ommastrephid cephalopod *Lycotheuthis diadema* also forms part of the diet (Smale, 1986). For yellowfin tuna feeding in offshore waters, the pelagic crab *Charybdis smithii* was found to be the dominant prey item (Potier et al., 2007; Romanov et al., 2009). Long-term dietary changes have been observed for open-water surface swimming skipjack and yellowfin tuna in the western-equatorial Indian Ocean, shifting from fishes to crustacea. During the 1980´s, the main prey item was the small cupleid *Engraulis japonicus* (Roger, 1994), whereas in the 2000s the stomatopod *Natosquilla investigatoris* was by far the dominant prey item (Potier et al., 2002, 2004) for yellowfin and skipjack tuna captured in the Seychelles archipelago.

Foraging depth also influences the type of prey consumed by tropical tuna species (Kornilova, 1980). The stomach content of surface swimming yellowfin and bigeye tuna was dominated by the stomatopod *N. investigatoris*. Additionally, surface caught yellowfin tuna showed preference for fish (scombrids) and bigeye tuna for squids (ommaestrephids) (Potier et al., 2004). Deep swimming bigeye tuna showed a generalized feeding behavior with no dominant prey species found in their stomach. For yellowfin tuna swimming in deep waters both types of feeding strategies were found (i.e. generalized and specialized), with specialized feeders favoring crustaceans such as crab larvae or the swimming crab *Charybdis edwardsi* (Potier et al., 2004). Specialized feeding behaviors have also been reported in reproductive females of yellowfin tuna from Atlantic, Pacific and Indian Oceans (Bard et al., 2002; Flynn and Paxton, 2013; Zudaire et al., 2015). During the spawning period, the latter seem to feed more intensively on lipid-rich fish, particularly on cigarfish, *Cubiceps pauciradiatus* (Zudaire et al., 2015).

Stomach content analyses also indicate differential diel feeding behavior among species (Fig. 7). Skipjack tuna feed during the day on prey that remain in shallower depths (0 to 200 m according to Roger, 1994), with a bimodal peak of feeding activity around crepuscular periods (Olson et al., 2016). Peak feeding of yellowfin and bigeye tuna occurs between 8 a.m. and 12 noon, although stomach fulness indices show that yellowfin tuna feed throughout the day, while bigeye tuna is, in general, a daytime feeder (Olson et al., 2016). Carbon and nitrogen isotopic signatures measured in muscles of the three species of tropical tuna in the western Indian Ocean, suggested that bigeye tuna have a higher trophic position than skipjack and yellowfin tunas (Olson et al., 2016; Sardenne et al., 2016). Due to their relative tolerance to lower temperature and oxygen levels, bigeye tuna are able to prey at greater depths and lower light intensity (Stobberup et al., 1998). Finally, skipjack tuna possess greater daily ratios of ingestion (3.5-4.2%, percentage of body weight per day), than yellowfin (1.1-2.0%) and bigeye (0.6-3.6%) tunas (Olson et al., 2016) .Research on the trophic ecology of tropical tuna of the western Indian Ocean indicate some degree of resource portioning both intra- and interspecifically, which allows the exploitation of different trophic niches and effectively reduces the potential for food competition.

3.3. Age and Growth

Several approaches have been used to estimate growth of tropical tunas, including modal analyses of length frequencies, the examination of daily and annual rings in calcified structures (e.g. otoliths, spines, vertebrae) and information obtained from tag and recapture data (for an exhaustive review see Murua et al., 2017). In addition, some growth models have combined the methods described above in an integrated model, with the aim of reducing the biases associated with any single approach (Dortel et al., 2015; Eveson et al., 2015).

Tropical tuna possesses a relatively high growth performance, characterized by having both high growth rate coefficients (k) and, in the case of yellowfin and bigeye tuna, high asymptotic fork lengths (L_∞). Skipjack tuna is considered the fastest growing species of all tunas (Murua et al., 2017). In the Indian Ocean, estimated k values range between 0.23 and 1.41 year^{-1} and L_∞ values from 60.6 to 94.8 cm FL, but most growth curves reported k values >0.4 and L_∞ <82.5 cm FL (Fig.8). Yellowfin tuna is the second fastest growing tuna species but has a higher growth performance than skipjack tuna. Reported k and L_∞ values in the Indian Ocean range from 0.18 to 1.54 and from 123.6 to 272.7, respectively (Murua et al., 2017). Mean reported k value was 0.34 and most L_∞ values were ~160 cm FL (Fig.8). Fewer studies have reported growth parameters of bigeye tuna in the Indian Ocean. They have slower growth rates than the other two tropical tuna species, reported k values ranging from 0.06 to 0.45, with a mean k of 0.22 (year^{-1}) (Murua et al., 2017). Reported asymptotic lengths range from 150.9 to 423.0 cm FL (Fig.8), although mean reported L_∞ values were ~190 cm FL. The large variations in growth parameter estimates among studies are probably due to the different techniques used (i.e. disagreements between otoliths and spines), size of analysed fish (i.e. different ages can produce different parameters), lack of inter-laboratory calibrations (i.e. different readers might produce different results), sampling strategy and/or sampling coverage (i.e. spatio-temporal variability in growth). All these factors caution against extrapolating the growth model outside the range of the data used for parameter estimation.

Previous studies have indicated that tropical tuna may pass through different stanzas of growth rates during their life (Fonteneau, 1980; Bard, 1984; Marsac, 1991). This hypothesis was revisited and supported by Dortel et al., (2015) and Eveson et al., (2015) for the three tropical species in the Indian Ocean. In the case of skipjack tuna, the two-stanza growth model is characterized by a rapid growth in the first stage, followed by a slower growth in the second stage (Eveson et al., 2012, 2015) (Fig.9a). Due to the initial high growth rates, skipjack tuna can reach ~45 cm FL in the first year of life, and between 50- 65 cm FL in the second year, from which the growth rates diminish (Tanabe et al., 2003). Similar results were obtained by Kayama et al., (2004) for skipjack in the eastern Indian Ocean (45 cm FL), although reported sizes for the second year were smaller (50-55 cm FL). By contrast, yellowfin and bigeye tuna have a phase of slower growth rate as juveniles, followed by a stanza of a higher growth rate. The first slow-growth phase in yellowfin tuna (around 2.1 cm month^{-1}) lasts until they reach 56-70 cm FL. After a quick transition, yellowfin tuna then grow at a faster rate (4.1 cm month^{-1}) until they reach approximately 145 cm FL, with a progressive decrease in the growth rate with size thereafter (0.01 cm month^{-1}) (Fig. 9b) (Olivier, 2002; Dortel et al., 2015; Eveson et al., 2015). In bigeye tuna, the transition between slow- and fast-growth phases occurs at a similar length (around 60 cm FL), however this transition is more gradual (Fig.9c) (Eveson et al., 2015). There is evidence for sexual-dimorphism in growth in Indian Ocean yellowfin and bigeye tuna (Stéquert et al., 1996; Nootmorn, 2004; Nootmorn et al., 2005; Zudaire et al., 2013a), with male individuals attaining larger maximum sizes compared to females (Farley et al., 2006; Shih et al., 2014; Eveson et al., 2015).

Bigeye tuna possess the greatest life expectancy among tropical tuna. Based on otolith interpretation and tagging studies, Farley et al. (2006) proposed a maximum age of at least 16 years for bigeye tuna caught in the eastern Indian Ocean, based on validated annual bands. Maximum age for skipjack however is ~6-7 years, whereas reported longevity for yellowfin tuna is in the order of 9 years in the Indian Ocean (Shih et al., 2014; Murua et al., 2017). However, bomb radiocarbon dating has recently validated age estimates of 16-18 years for yellowfin tuna in the Atlantic Ocean (Andrews et al., 2020). After this, our understanding on maximum ages of yellowfin tuna in the Indian Ocean should be revisited.

3.4. Reproductive biology

Tropical tunas are oviparous, have an asynchronous oocyte development and spawn multiple batches of oocytes each spawning season (Joseph, 1963; Hunter et al., 1986; Stéquert and Ramcharrun, 1995; Schaefer, 2001). In terms of reproductive strategy, female skipjack tuna follow what has been described as an income breeder strategy, that is, required energy is obtained directly from food intake rather than from accumulated energy reserves (Grande et al., 2016). Female yellowfin tuna however, are considered to be mixed income-capital breeders (Zudaire et al., 2014). Analyzing lipid allocation of yellowfin tuna from the western Indian Ocean, Zudaire et al., (2014), found that required energy for gonad development depended mainly on the energy provided by feeding during the prolonged spawning period and, to a lesser extent, on stored lipids. For bigeye tuna, there are no studies addressing the breeding strategy and energy allocation to reproduction in the Indian Ocean. However, Sardenne et al., 2017 suggested an income-capital breeding strategy for bigeye tuna after concluding that liver neutral fatty acids levels were similar to those from yellowfin.

Mean size at maturity, i.e., length at which 50% of female skipjack tuna are classed as mature (L_{50}), has been estimated at between 39.9 cm and 42.0 cm FL in the western Indian Ocean (Stéquert, 1976; Grande et al., 2014). In the case of yellowfin tuna, L_{50} values range between 75 and 114 cm FL. In the western Indian Ocean, L_{50} of yellowfin tuna was estimated at 75.0 cm to 102.0 cm FL, depending on the threshold oocyte development stage considered to indicate maturity (i.e., cortical alveolar vs. vitellogenic) (Zudaire et al., 2013a). In the eastern and west-central Indian Ocean, L_{50} for females has been estimated at 109.6 cm and 114.0 cm respectively, whereas L_{50} reported for males was at 104.9 cm and 120.0 cm FL (Nootmorn et al., 2005; Zhu et al., 2008). Similarly, different L_{50} estimations have been reported for bigeye tuna in the Indian Ocean. Mean size at maturity estimates range from 88.1 cm FL (females) and 86.8 cm FL (males) in the eastern Indian Ocean (Nootmorn, 2004) to 102.0 (females) and 119.3 (males) cm FL in the western Indian Ocean (Zhu et al. 2011; Zudaire et al. 2016).

Tropical tuna show an indeterminate fecundity type (i.e., oocyte maturation is continuous during their extended spawning periods) (Grande et al., 2012; Zudaire et al., 2013b). Studies carried out in the western Indian Ocean show that skipjack tuna has a higher mean relative batch fecundity, 140.0±64.0 oocyte g^{-1} of gonad-free weight (Grande et al., 2014), than yellowfin, 74.4 oocyte g^{-1} of gonad-free weight (Zudaire et al., 2013a), and bigeye tuna, 11.5±7.1 oocyte g^{-1} of gonad-free fish (Zudaire et al., 2016). Reported individual fecundity for skipjack tuna range from 80,000 oocytes for a 44 cm FL female to 1.25 million oocytes for a large (75 cm FL) female in the western Indian Ocean (Stéquert and Ramcharrun, 1995). Grande et al. (2010) estimated batch fecundity from 100,828 oocytes to 627,325 oocytes in female skipjack ranging from 32 to 68 cm FL. In the case of yellowfin tuna, estimated batch fecundity varied from 0.3 to 5.3 million oocytes in females from the eastern Indian Ocean (Nootmorn et al., 2005). In the western Indian Ocean mean batch fecundity for female yellowfin tuna 79-147 cm FL was estimated at 3.1 million oocytes (Zudaire et al., 2013a). Finally, mean batch fecundity of bigeye tuna in the western Indian Ocean has been estimated at 0.75±0.52 million oocytes (Zudaire et al., 2016). Spawning frequency of tropical tuna species in the Indian Ocean has not been reported yet, but in the Pacific Ocean the mean spawning interval has been determined as 1.18 , 1.53 and 1.09 days for skipjack, yellowfin and bigeye tuna respectively (Schaefer, 2001).

Timing of spawning varies in relation to the geographical distribution of the three species of tropical tuna (Table 1). In the western Indian Ocean, spawning of skipjack tuna occurs throughout the year, with peaks of intensity between November-March and June-July, coinciding with the northeastern and southwestern monsoon period respectively (Stéquert et al., 2001; Grande et al., 2014). Koya et al., (2012) also observed year-round spawning in Indian waters but reported a peak in activity between December-March and a smaller peak from June to August. Spawning period seems to shorten as the distance from equator increases (Matsumoto et al., 1984). Yellowfin tuna predominantly spawn from November to February in equatorial waters, primarily on spawning grounds west of 75°E (Shung, 1973; Hassani and Stéquert, 1991; Zudaire et al., 2013a). A shorter spawning period (i.e., from December to February) has been reported for females smaller than 100 cm FL (Zudaire et al., 2013a). The offshore waters of Mozambique Channel and the eastern Indian Ocean are also known as secondary spawning grounds. In the east, spawning is prolonged from November until April (John, 1995; John et al., 1998; Nootmorn et al., 2005). Secondary spawning peaks have also been described; in June for the western Indian Ocean, between April and June around Sri Lanka, and from October to December off northern Australia and Madagascar (Stéquert and Marsac, 1989; Stéquert et al., 2001; Zudaire et al., 2013a). Bigeye tuna from different areas of the Indian Ocean possess differences in spawning seasonality. In equatorial waters of the Indian Ocean, bigeye tuna are able to spawn year round (Kume et al., 1971; Stobberup et al., 1998). In the eastern Indian Ocean, the spawning season is reported from December to January, with another peak in June (Nootmorn, 2004), whereas in the western Indian Ocean, high reproductive activity has been observed from January to March (Zudaire et al., 2016).

4. Stock structure

There is little information available to determine whether the tropical tuna of the Indian Ocean constitute single or several stocks. Current stock assessments are conducted assuming that there are single, Indian-wide stocks of skipjack, yellowfin, and bigeye tuna; and that there is no exchange of fish among Atlantic, Indian and Pacific Oceans. This assumption is based on the results obtained from the Indian Ocean Regional Tuna Tagging Program (RTTP-IO) that suggest rapid and large-scale movements of the three tropical species in the Indian Ocean (Fonteneau and Hallier, 2015). However, findings obtained from other approaches (e.g. fishery data and genetic markers) show a more fragmented population structure than typically assumed in the assessment and management of these species. The aim of this section is therefore to compile and evaluate the scientific evidence available on Indian Ocean skipjack, yellowfin, and bigeye stock structure.

4.1. *Fisheries Data*

Spatial and temporal distribution of catch and effort data from the commercial fishery can be used as a crude indicator of stock structure if, for example, strong geographic differences in age composition, relative abundance and/or distribution are reported. Early studies used catch data distribution and fishery length data of skipjack, yellowfin and bigeye tuna to describe the stock structure in the Indian Ocean. A study based on size composition of skipjack caught by longline vessels in the Indian Ocean during 1972-1975, reported relatively smaller specimens in the central and eastern Indian Ocean (Pillai and Silas, 1979). Similarly, analysing Japanese longline fishery data (1961-1965), Morita and Koto, (1970) suggested a two-stock structure for the Indian Ocean yellowfin tuna; the western and eastern stocks separated approximately at 100°E and possibly mixing in adjacent waters. Later, Nishida (1992) concluded that there were two major and two minor stocks of yellowfin tuna in the Indian Ocean, using catch-per-unit-effort (CPUE), age-specific CPUE and size variations obtained from longline fishery data. The two major stocks (named western and eastern) were defined at 40°-80°E and 80°-120°E respectively. The two minor stocks were defined westward 40°E and eastward of 120°E, and named far western and far eastern respectively, with the latter possibly being part of the Pacific stock. In the case of the bigeye tuna, a single stock was suggested for the Indian Ocean, based on the distribution, size composition and sexual maturity of the fish, although some differences between eastern and western bigeye tuna were reported (Kume et al., 1971).

4.2. *Morphometric and meristic characters*

Phenotypic variation in anatomical characters have historically been used for stock identification purposes. Morphometrics analyse quantitatively the size and shape of the body, whereas meristic analyses refer to countable traits (e.g. fin rays, scales in rows, gill-rakers and myomeres). By comparing different body characters of yellowfin tuna collected from six grounds in the Indian Ocean, Kurogane and Hiyama (1958) suggested a 3-stock structure, one stock in the western Indian Ocean and two in the eastern Indian Ocean, with a strong intermingling between 80-100°E. Although a preliminary study demonstrated the potential utility of otolith shape variation for skipjack tuna stock structure identification in the Indian Ocean (Wujdi et al., 2017), this marker has not yet been used for tropical tuna stock structure analyses in this ocean.

4.3. Parasites

Geographical variation in species composition and abundance of parasites has been used as a natural tag for fish stock structure analyses. This is because parasite occurrence depends on biogeography, distinct environmental tolerances of parasites, differential availability of intermediate hosts, and basically different life history characteristics of the fish stocks *per se* (Catalano et al., 2014). Lestari et al. (2017) found 7 potential parasites that might be useful to discriminate juvenile yellowfin and bigeye tuna from Indonesian waters. More recently parasite data from juvenile yellowfin and bigeye tuna from the Maldives proved to be significantly different from those belonging to Indonesian waters (Moore et al., 2019). Therefore, authors have suggested movements of yellowfin and bigeye from the Maldives archipelago into the eastern Indian Ocean were limited.

4.4. Genetics

With the development of new molecular techniques, the use of molecular markers such as allozymes, mitochondrial or nuclear DNA polymorphisms have increased in stock identification studies. Each of these markers presents a series of advantages and limitations, but all have been used in Indian Ocean tropical tuna stock structure studies. Often, the use of different techniques and sampling designs provide contradictory results, especially when the organism being studied has a widespread distribution and/or complex natural history, as is the case of skipjack, yellowfin and bigeye tuna (Kumar and Kocour, 2015).

For example, Menezes et al. (2006) found high levels of genetic differentiation between skipjack tuna collected from the east coast of India and the coast of Japan (Pacific Ocean) after using PCR-RFLP analysis of the mitochondrial D-loop region. However, when using nuclear microsatellite markers, there was no differentiation between samples from the two aforementioned regions (Menezes et al., 2008). Also at the inter-oceanic scale, Fujino et al. (1981) found significant differences in allozyme allele frequencies in skipjack from the Indian Ocean compared to those collected both from the Atlantic and western Pacific Oceans. Additional studies comparing Atlantic and Pacific Ocean skipjack tuna revealed a high degree of genetic similarity among these two oceans (e.g. Graves et al., 1984; Ely et al., 2005). Few genetic studies have been conducted on skipjack tuna population structure within the Indian Ocean to date. Although limited to a regional scale, these studies reported the presence of heterogeneous groups of skipjack in the north-central and eastern Indian Ocean. In adjacent waters of Sri Lanka, Maldives and Laccadive islands, two differentiated stocks have been described after analysing patterns of genetic variation with both a mitochondrial gene and six microsatellite loci (Dammannagoda et al., 2011). Additionally, sequence data of the mitochondrial D-loop region revealed the presence of four clades of skipjack tuna in the east and west coasts of India (Menezes et al., 2012). Although both studies failed to find a clear spatial pattern among samples, Dammannagoda et al. (2011) proposed different hypotheses for the physical mixture of these two distinct skipjack tuna clades around Sri Lanka: (i) different stocks may spawn in distant areas of the Indian Ocean, and juveniles subsequently separately migrate towards Sri Lanka, which is a highly productive foraging ground and (ii) the monsoonal currents in the Indian Ocean could drive the larvae towards this area by passive transport. Menezes et al. (2012) suggested that the absence of a symmetrical pattern of haplotype distribution in the analysed clades could be due to secondary contact and interbreeding of populations after being geographically isolated for a prolonged period. In the eastern Indian Ocean, the results from three microsatellite loci suggest the presence of two stocks of skipjack tuna in Indonesian waters, with genetic differentiation between skipjack from west of Sumatra and south of Java (Jatmiko et al., 2019).

In the case of yellowfin tuna, the use of different genetic markers has also lead to discordances both at intra- and inter-oceanic patterns of differentiation (Pecoraro et al., 2016). Using allozyme markers, Smith et al. (1988) described genetic heterogeneity between yellowfin tuna from the Pacific and Indian Oceans. However, Wu et al. (2010) did not detect any genetic differentiation between yellowfin tuna from the western Pacific and western Indian Oceans using mitochondrial markers. A global genetic study of yellowfin tuna combining both allozymes and mitochondrial DNA, suggested differentiation between the Atlantic, Indian, west-central Pacific and east Pacific oceans (Ward et al., 1997). Recently, the use of next generation sequencing has shed new light on the global population structure of yellowfin tuna. Using genomic wide single nucleotide polymorphisms (SNPs), Pecoraro et al. (2018) identified genetic differentiation of yellowfin tuna between Indian, Atlantic and Pacific Oceans. Moreover, genomic analyses have revealed asymmetrical dispersal from the Indian Ocean yellowfin tuna into the Atlantic and highlighted that yellowfin tuna found along all the South African coast are derived from the Indian population (Barth et al., 2017; Mullins et al., 2018). This connection was also noticed during the RTTP-IO with a few yellowfin tuna tagged in Tanzania that were recovered in the southern Agulhas current, along the South African coasts. In light of this evidence, Mullins et al. (2018) proposed that the current operational boundary for management between the Atlantic and Indian stocks should be revisited. Using genome wide SNPs, Barth et al. (2017) found genetic differentiation of yellowfin tuna from the Arabian Sea with respect to those from the Atlantic and Indo-Pacific. Results from genome wide SNPs also indicate a marked genetic difference between samples from the central Indian Ocean (Maldives) and the western Pacific Ocean, but not between samples from eastern Indian Ocean (Indonesia) and the western Pacific Ocean (Proctor et al., 2019). Proctor et al. (2019) proposed that the observed pattern of differentiation may indicate limited gene flow between the central and eastern Indian Ocean, with more pronounced gene flow among Indonesian and Western Pacific regions. At intra-oceanic scale, the comparison between samples from the westernmost and easternmost parts of the Indian Ocean, did not reveal any genetic differentiation (Chow et al., 2000a; Nishida et al., 2001). In contrast, mitochondrial and nuclear microsatellite loci variations of yellowfin tuna collected from six fishing grounds around Sri Lanka and one in Maldives, suggested the existence of discrete yellowfin tuna populations in the northwest Indian Ocean (Dammannagoda et al., 2008). Additionally, a study using the mitochondrial D-loop region supported the presence of three genetically different stocks of yellowfin tuna in the north Indian Ocean (Kunal et al., 2013).

Global genetic studies have also reported an inter-oceanic division between Atlantic and Indo-Pacific bigeye tuna both by analysing nuclear (Durand et al., 2005) or mitochondrial (Alvarado-Bremer et al., 1998; Chow et al., 2000b; Martinez et al., 2006) markers. Indo-Pacific bigeye tuna intermingle off southern Africa with Atlantic bigeye tuna (Chow et al., 2000b; Durand et al., 2005). However, Gonzalez et al., 2008 found discordant results when analysing genetic structuring and migration patterns of Atlantic bigeye tuna. Microsatellite loci supported a single worldwide panmictic bigeye tuna population, whereas mitochondrial markers show genetic differentiation between Atlantic and Indo-Pacific bigeye tuna populations, as previous studies did. However, a recent study using SNP data proved restricted connectivity between Indian Ocean (central and eastern) and the western Pacific Ocean bigeye tuna, with samples from central Indonesia having limited connectivity also with the previous areas (Proctor et al., 2019). Few studies have been carried out to describe the structure of bigeye tuna in the Indian Ocean. Most of them did not observe signs of heterogeneity, supporting the existence of a single panmictic population in this ocean. After analysing variations in mitochondrial DNA polymorphisms and seven microsatellite loci of bigeye tuna distributed in the eastern, central and western Indian Ocean, minimal and generally non-significant genetic differentiation was reported (Appleyard et al., 2002). Likewise, a study using mitochondrial DNA data from bigeye tuna sampled among 4 regions (Cocos Islands, south-eastern Indian Ocean, south-western Indian

Ocean and Seychelles) failed to detect any differences between areas (Chiang et al., 2008). A local study carried out in distinct locations off Indonesia however, reported the existence of two genetically distinct groups of bigeye tuna in the eastern Indian Ocean, based on genetic distances and RFLPs mitochondrial D-loop region (Nugraha et al., 2010). Similarly, SNP analyses indicated a gradient in geneflow between the Indonesian archipelago, the eastern Indian Ocean, and the Maldives, consistent with an isolation by distance model (Proctor et al., 2019).

Overall, it seems that results obtained from the application of a single type of molecular marker should be interpreted with caution. For the three species of tropical tunas, different population structure was suggested depending on the analyses. In general, results relying on mitochondrial DNA showed higher heterogeneity than those based on nuclear DNA. Qiu et al. (2013) hypothesized that this mito-nuclear discordance found in tuna species, may be a result of behavioural differences between sexes rather than a misuse of the chosen marker; mitochondrial DNA is inherited from females which may present greater philopatric behaviour. If so, female philopatry would have enhanced mitochondrial DNA diversity, while male-biased dispersal would have homogenized group differences that could be revealed in the nuclear genome (Qiu et al., 2013). The current rise of next generation sequencing (NGS) based genotyping methods, presents a cost-effective alternative to increase the precision in detecting small genetic differences (Rodríguez-Ezpeleta et al., 2019). At local scale, NGS techniques have been already used to discriminate among yellowfin tuna populations of the Pacific Ocean (Grewe et al., 2015). To date no studies of that kind have been published in the Indian Ocean. It is recognised that this technique, combined with a structured basin-wide sampling design, would provide a powerful tool to finally reveal a clear picture of the population structure of tropical tunas in this ocean.

4.5. Otolith microchemistry

Chemical composition of fish otoliths and other calcified structures (e.g. scales, fin-rays and spines), have been recognised as useful natural markers to discriminate among groups of fish that have inhabited different environments. While genetic analyses provide information over evolutionary timescales, otolith chemistry inform over ecological time frames (i.e., larval history, individual life span…) (Campana, 1999, 2005; Tanner et al., 2016). Thus, this technique is useful to identify differences in natal origin or migration patterns, revealing complex population structures and biologically meaningful units. Despite their importance to delineate fish stocks, otolith microchemistry has barely been used in tropical tuna structure analyses. Natal origin studies have been conducted for bigeye tuna of the Pacific Ocean (Rooker et al., 2016), and for yellowfin tuna both in the Pacific (Wells et al., 2012; Rooker et al., 2016) and the Atlantic Oceans (Shuford et al., 2007; Kitchens, 2017). Arai et al. (2005) described movements and life history patterns of skipjack tuna in the Pacific Ocean based on otolith Sr:Ca ratios. In the Indian Ocean, initial investigations of otolith trace element data proved useful for yellowfin tuna stock delineation (Artetxe-Arrate et al., 2019). Moreover, the study detected some level of separation between two potential nursery regions (Seychelles-Somalia and Mozambique Channel) using young-of-the-year (YOY) yellowfin tuna from the western Indian Ocean. Similarly, otolith microchemistry analyses showed restricted movements of yellowfin and bigeye tuna of the eastern Indian Ocean during their first 4-6 months of life (Proctor et al., 2019). Otolith isotopic analyses, and particularly oxygen isotope δ_{18}O composition, might also be useful in discriminating among fish of different origins in the Indian Ocean (Fig.10). Both techniques need now to be expanded at ocean basin scale, to help clarify unresolved population structure of the three species of tropical tuna in this ocean.

4.6. Tagging

Artificial tags have commonly been used as an indirect approach to identify stock structure. Tagging provides information of fish dynamics (e.g. movement range and pattern), and hence can be a useful tool to infer the degree of mixing among potential stocks. There is an extensive tagging data collection in the Indian Ocean, as tagging programs were initiated in the Maldives in 1990-1994 and continued 15 years later (2005) when the IOTC started a large-scale Indian Ocean Regional Tuna Tagging Program (RTTP-IO) (Murua et al., 2015).

Results obtained from these programs describe fast and large-scale skipjack movements, with an average monthly distance of 1066 miles between tagging and recovery positions in the first year (Fonteneau and Hallier, 2015). Skipjack tagged in Tanzania showed the larger and fastest migrations (e.g. average distances of 1129 miles after one month at liberty), followed by skipjack tagged in Mozambique Channel (an average of 894 miles travelled). Despite the rapid movements described for skipjack tuna tagged in the Mozambique Channel, most tagged tuna returned to this area within one year, coinciding with the March-May fishing season, a pattern that was recurrent over the studied years (Fonteneau and Hallier, 2015). Authors suggested that rather than a random movement, this return may correspond to a fidelity behavior towards a feeding area. Average distances travelled were shorter in the Seychelles tagging (698 miles) and the lowest for skipjack tuna tagged in the Maldives (358 miles) (Fonteneau, 2014). This result is very similar to the results of the early Maldivian tagging program carried out between 1990 and 1995 (Adam and Sibert, 2002). Although the heterogeneity of skipjack movement patterns was high, Adam and Sibert (2002) found evidences of low emigration rates from Maldives to the rest of the Indian Ocean. This could be because skipjack tuna travel longer distances in the open ocean than in archipelagic waters (Fonteneau, 2014). This is the case for the Maldives, which comprises a network of nearly 1200 islands. In addition, the presence of numerous anchored FADs in this region, under which skipjack aggregate, may be reinforcing the “island effect”, reducing the distance travelled by this species. Conversely, drifting FADs may increase the mobility of skipjack in other areas (Marsac et al., 2000; Hallier and Gaertner, 2008). Thus, based on these results, Fonteneau (2014) proposed that future stock assessment of the skipjack population should consider at least 4 different regions with differential mixing rates in the Indian Ocean: southwest Indian Ocean, northwest Indian Ocean, central Indian Ocean and eastern Indian Ocean.

The evidence of fast and large movements of yellowfin tuna reported by the RTTP-IO supports the assumption of a single well-mixed yellowfin tuna population within the Indian Ocean (IOTC, 2017c). For instance, short-term recoveries were associated with relatively long distances (249 miles on average), about 5 times longer than the distances of short-term recoveries in other oceans (Fonteneau and Hallier, 2015). Past tagging studies showed that there was exchange of yellowfin tuna between the central and the western Indian Ocean (Yano, 1991) and movements of yellowfin from Maldives to Sri Lanka (Nishida et al., 1998). However, Kolody and Hoyle (2013) found that tag releases from the Maldives area were sometimes retained there, without mixing into the rest of the population. It is also noteworthy that most tagging events occurred in the western part of the Indian Ocean and few recoveries have been reported from the eastern part. Langley and Million (2012) suggested that the 28-29ºC SST isotherm may limit the eastward dispersal of the tagged fish. Thus, there may be some degree of separation between the yellowfin tuna populations of the west and east Indian Ocean.

Results obtained from the RTTP-IO also describe fast and large-scale bigeye movements. The average monthly distance between tagging and recovery positions is 918 miles in the first year, with distances increasing slowly in subsequent years (Fonteneau and Hallier, 2015). For instance, bigeye released off Tanzania were subsequently recovered as far away as the subtropical Indian Ocean, eastern Indian Ocean and the southern and western coasts of South Africa (Hallier and Million, 2012). The reported fast and extensive movements of bigeye tuna in the Indian Ocean led to the assumption that its population is highly mobile, supporting the current assumption of a single stock for the Indian Ocean (IOTC, 2017a).

Conventional tagging studies, however, depend on tag-recapture efforts, and can be sensitive to the distribution of releases and assumptions related to the tagged population (e.g. random selection, independence and complete mixing) (Pollock and Pine, 2007; Berger et al., 2014). This may lead to biased results and data misinterpretation. Fonteneau and Hallier (2015) advised that current tagging programs targeting tropical tuna, may still not be adequate to estimate the potential stock mixing rates. For instance very few tags have been returned from the eastern Indian Ocean (Murua et al., 2015), which may reflect a lack movement from west to east, but more certainly, this is a consequence of poor reporting rates by longliners operating in the east Indian Ocean. Therefore, movement dynamics within the eastern Indian Ocean have not yet been adequately evaluated. Electronic tags may present a complementary platform to elucidate tropical tuna real movements. This technique proved to be useful in identifying population structure in other tuna species (Block et al., 2005). Finally, an accurate knowledge of tropical tuna movements in the Indian Ocean will be essential to establish management boundaries if different stocks are revealed.

5. Conclusions and future research directions

Since tropical tuna fisheries of the Indian Ocean play an important role in the three sustainability pillars (i.e., social, environmental and economic) of the region, there is an urgent need to advance our understanding of the resource and the fisheries to ensure a proper and sustainable management of these species (Asche et al., 2018). Scientific advice on tropical tuna of the Indian Ocean is based, among others, on the results of the stock assessment models. However, more accurate and comprehensive fishery data statistics, which cover all fisheries components, are needed to improve the monitoring and stock evaluation of these species which will, in turn, reduce the uncertainty of the assessment and improve the scientific advice for management. IOTC should, therefore, prioritize the capacity of the countries in the region to implement monitoring systems. This will allow to collect fishery statistics that contribute to the provision of the scientific advice for management of IOTC species. Strong monitoring systems, once implemented, will also ensure a better control mechanism to enforce any agreed management measure by IOTC (e.g. yellowfin catch limits and skipjack annual quota). Here, available information regarding Indian Ocean yellowfin, skipjack and bigeye tuna fisheries, life history and stock structure has been reviewed. This will help identify gaps in our knowledge that need to be filled to improve the assessment and management advice for these resources.

Firstly, there is, in general, a lack of information regarding life-history traits of skipjack, yellowfin and bigeye tuna at an oceanic scale in the Indian Ocean. Most studies are regionally limited, which impedes a global overview of the complex interaction between the environment and these species and makes it difficult to incorporate life-history parameters at the appropriate scale into stock assessment models. Studies that characterize fundamental life-history characteristics (e.g. growth and reproductive parameters) at ocean scale are needed to understand if differences stem from regional differences or just from different sampling strategies. Growth, mortality and reproduction are determinant factors for population productivity and, thus, key variables for stock assessment and management advice (Maunder et al., 2015). However, there are discrepancies regarding the growth and reproduction parameters of these key species in the Indian Ocean, which increases uncertainties in assessments of their status and advice for their management. Moreover, the fact that different studies calculate growth models based on fish from different size/age classes, caution the extrapolation of the results outside the range of the data. Therefore, future studies should ensure that sampling covers the full length-range of fish in the population to better inform stock assessment. Despite strong evidence of sexual-dimorphism in yellowfin and bigeye tuna growth (Eveson et al., 2015), which can lead to elevated sex-biased fishing mortality rates, this is not currently being considered in stock assessments due to a lack of the necessary data. Similarly, there is still not a consensus on spawning time and location of tropical tuna in the Indian Ocean, which is important to inform assumptions about total reproductive output. In order to move towards ecosystem-based fisheries management (EBFM), a better understanding of the habitat utilization and trophic relationships of the three tropical tuna in the Indian Ocean is also needed. Expanding the knowledge of vertical movements of these species would be useful to evaluate the species-specific and/or age class vulnerability to different fishing gears (e.g. purse-seine and longline) in the Indian Ocean and evaluate the impacts of FADs and potential utility of alternative management measures. Besides, a comprehensive approach that combines stomach content data, trophic markers (e.g. stable isotopes, mercury, lipid classes and fatty acids), and fish condition indices will allow delineation of trophic pathways for skipjack, yellowfin and bigeye tuna from the Indian Ocean. This information will be essential in understanding the effect of human induced pressures, such as fishing, climate change or the impact of the deployment of FADs, on these species. For example, skipjack tuna have fast growth rates and reach sexual maturity the fastest among three tropical tuna species (Murua et al., 2017) and, hence, it is considered more resilient and less susceptible to overfishing than yellowfin and bigeye tuna. However, Worm and Tittensor (2011) reported that skipjack tuna has undergone distribution range reduction in the Indian Ocean, contrary to what occurred in the Pacific Ocean. Although is very difficult to establish the scale and ultimate cause of the observed range change in skipjack tuna, an understanding of habitat preferences, species interactions, climate change and variability and other factors can contribute to a better understanding of their population dynamics and resilience to fishing pressure.

Secondly, the current assumptions of single stocks for yellowfin, skipjack and bigeye tuna in the Indian Ocean, are based on the latest result of tag-recoveries from the RTTP-IO, which provide evidence of rapid and large-scale movements for these tuna species. However, tagging events do not represent the whole Indian Ocean. Moreover, the distances between tag release and recovery positions do not provide a full picture of the real movements of tagged tunas, which can, more effectively, be tracked by electronic tagging. Indeed, other methods should also be considered for realistic stock structure determination. With the advent of NGS methods, a comprehensive study of these tropical tuna genetic structures using genome-wide highly informative SNP markers should be an important additional source of information to establish the underlying population structure. Natural markers, such as parasite tags or otolith microchemistry, can inform about the degree of connectivity over an ecological time scale (i.e. individual life span)and hence provide information on the environmental history experienced by individuals throughout different life stages. Therefore, they can contribute valuable insights of population structuring and highlight migration behaviours or population dynamics that might be sufficiently independent to guarantee spatially structured management. As each method provides information about stock structure at different spatial and/or temporal scales, the combination of different approaches has proved to be a powerful and reliable way to clarify unresolved questions related to stock structure (Welch et al., 2015; Pita et al., 2016; Izzo et al., 2017; Proctor et al., 2019) Thus, a holistic study that integrates results gained from several methods including different spatial and temporal scales, will be beneficial in defining appropriate units for the management of tropical tuna species in the Indian Ocean.

In summary, a broad-ranging collaborative program of research and data collection covering the complete distribution and life-history of the skipjack, yellowfin, and bigeye tuna in the Indian Ocean, should be carried out to improve stock assessment. These studies should be done together with the implementation of different and complementary stock delineation methods to establish the most realistic stock structure of the three tropical tuna species in the Indian Ocean, because species response to management decisions cannot be accurately predicted if the boundaries that characterise the stock are not correctly defined. Ultimately, an incorrect characterization of both life history parameters and stock structure perspectives may mislead the productivity and management of these globally important species. For example, if distinct stocks do exist, management measures based on the single stock assumption may lead to overexploitation and eventual collapse of less productive stocks. Therefore, an increased knowledge of these species' life-history characteristics and an accurate validation of stock structure of tropical tuna fisheries in the Indian Ocean will be essential to implement and enforce management strategies that ensure long-term sustainable fisheries.

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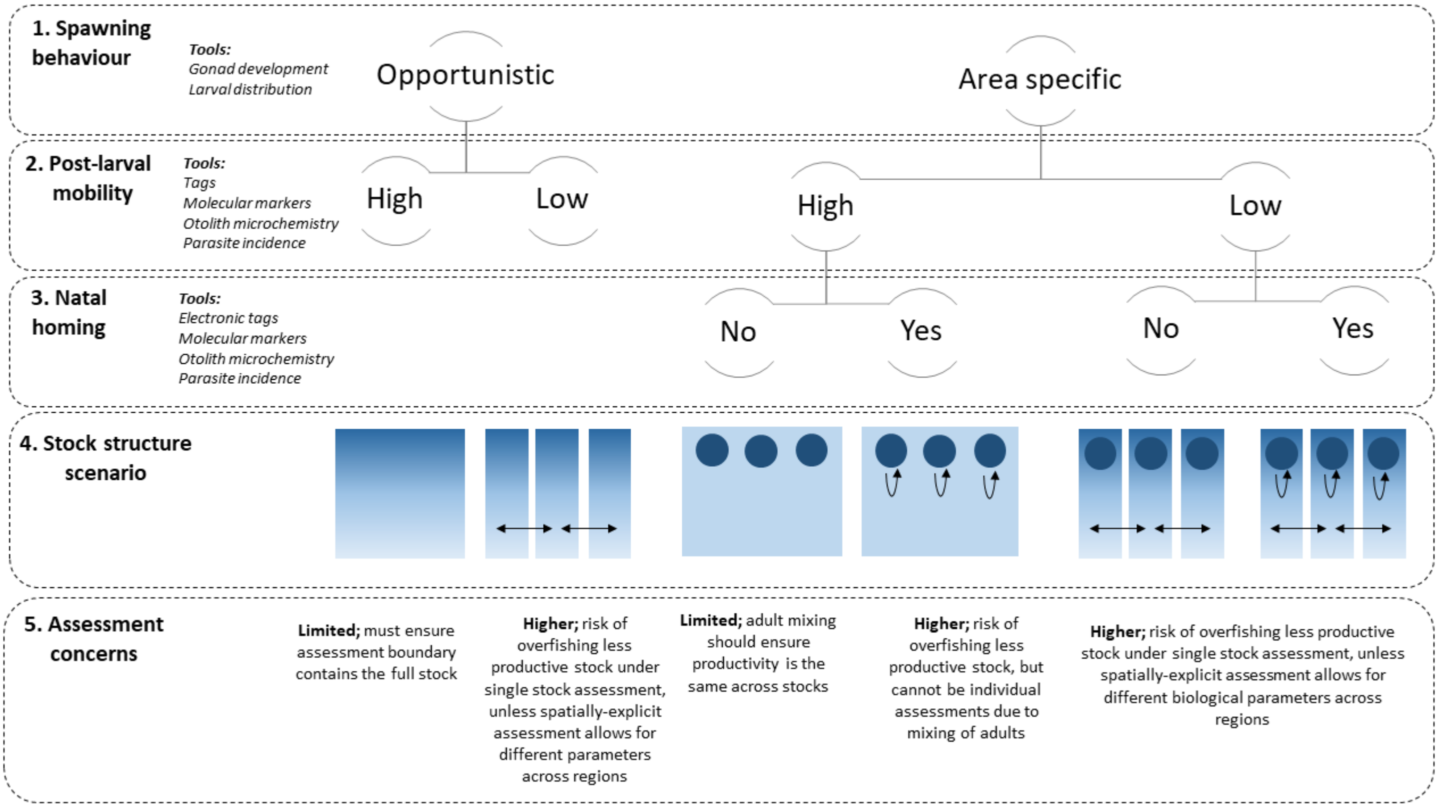

Figure 1. Conceptual summary of key research themes necessary to clarify the stock structure of tropical tuna species in the Indian Ocean; (1) spawning conditions (opportunistic vs. discrete), (2) post-larval mobility (low vs high) and (3) natal homing (yes vs no). Different combinations lead to different scenarios of stock structures (4), associated with potential stock assessment concerns (5). Stock structure diagrams indicate spawning areas (dark blue) within the overall distribution range (ligth blue) of the species. Main tools to study each research theme are also indicated. This figure is an adaptation from (SPC FAME, 2019).

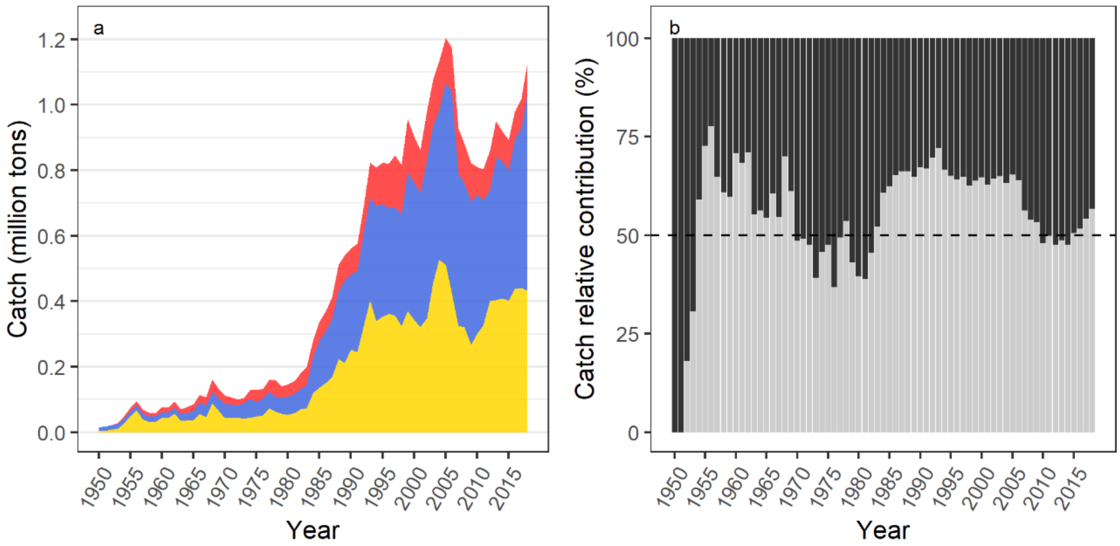

Figure2. Evolution of tropical tuna catches in the Indian Ocean over the 1950-2018 period; (a) Catch trends of, bigeye *Thunnus obesus* (red), skipjack *Katsuwonus pelamis* (blue) and yellowfin *Thunnus albacares* (yellow) in the Indian Ocean, (b) Relative contribution (% of total catches for each year) from the artisanal (light grey) vs industrial fisheries (dark grey). Data source: Indian Ocean Tuna Comission (IOTC) (avaible at: https://www.iotc.org/data/datasets/latest/NC).

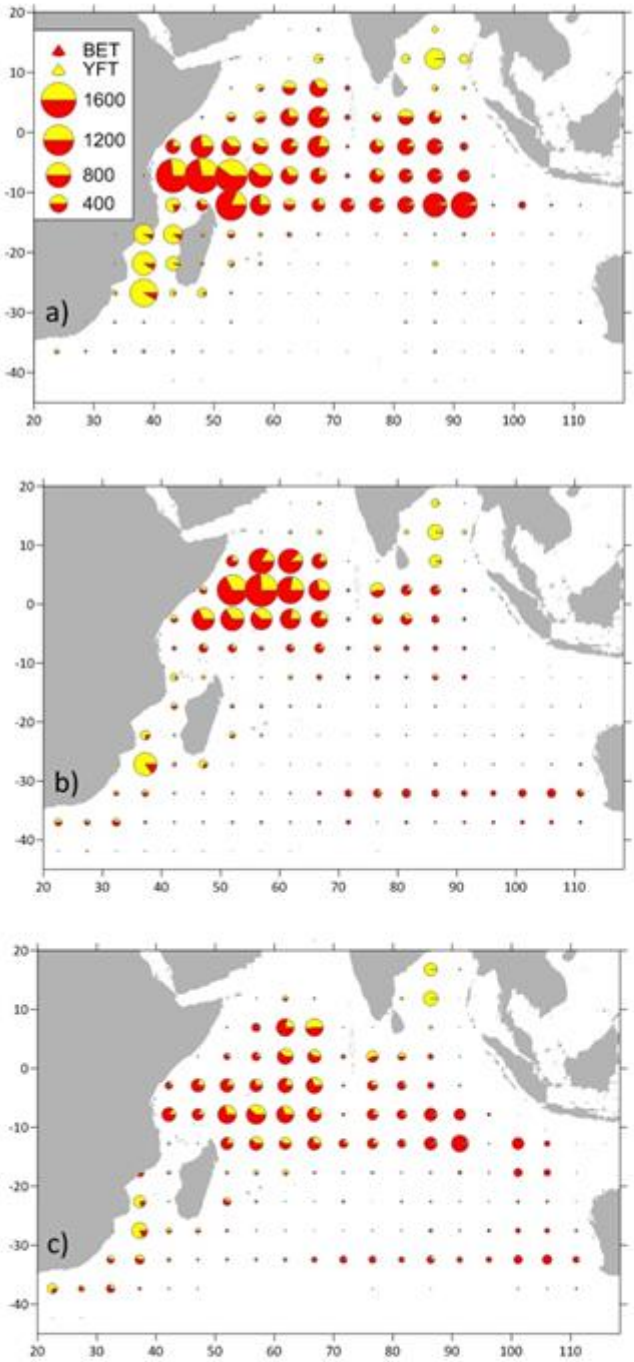

Figure 3. Average spatial distribution of longline catches over 2010-2017 for the months November-February (a), March-June (b) and July-October (c). Circles are plotted on a 5°x5° grid and pies are proportional to the catch by species (yellow: yellowfin; red: bigeye). The spatialized data originate from the Indian Ocean Tuna Comission, IOTC (avaiable at: http://www.iotc.org/documents/all-ce-files) but as they are incomplete, they have been raised to the nominal catches by applying raising factors established by fleet, year and species. A few data were available by 1°x1° and they have been aggregated on a 5°x5° grid to enhance visibility.

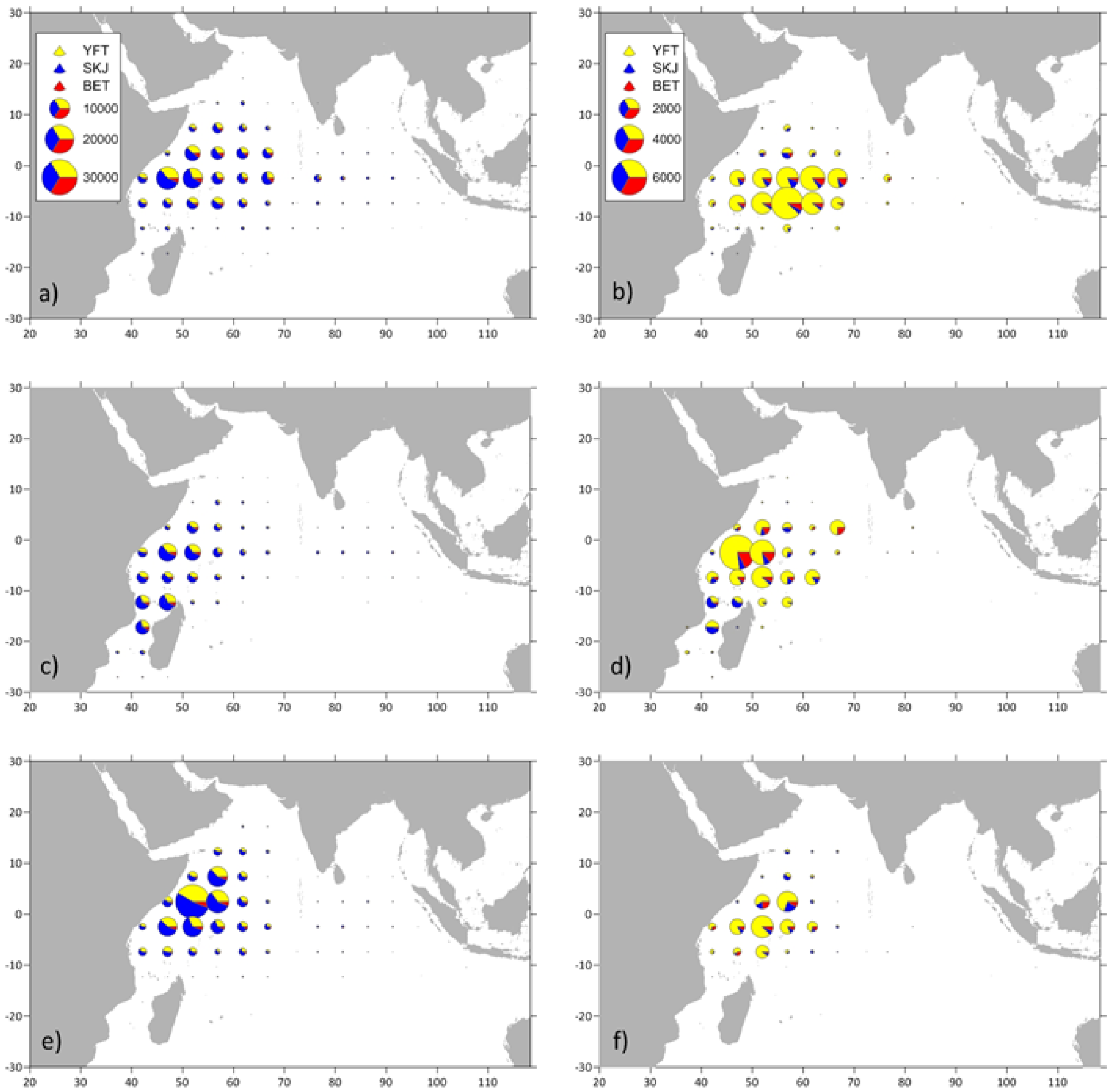

Figure 4. Average spatial distribution of purse seine catches over 2010-2017 for the months November-February (a,b), March-June (c,d) and July-October (e,f). Left column (a,c,e) show catches on floating objects, while right column (b,d,f) represent catches on free-swimming schools. Circles are plotted on a 5°x5° grid and pies are proportional to the catch by species (yellow: yellowfin; blue: skipjack; red: bigeye). Note the different scales and maximum between floating objects and free-swimming schools. The spatialized data originate the Indian Ocean Tuna Comission, IOTC (avaiable at: http://www.iotc.org/documents/all-ce-files) but as they are incomplete, they have been raised to the nominal catches by applying raising factors established by fleet, year and species. Purse seine data are mostly available by 1°x1° and they have been aggregated on a 5°x5° grid to enhance visibility.

Figure 5. Phylogenetic tree of the Scombridae family, which consists of 15 genera and 51 species, among which the three main species of tropical tuna, yellowfin (*Thunnus albacares)*, bigeye (*Thunnus obesus)* and skipjack tuna (*Katsuwonus pemalis)* are found (Collette et al., 2001). The sub-genus branch is based on findings from Díaz-Arce et al. (2016).

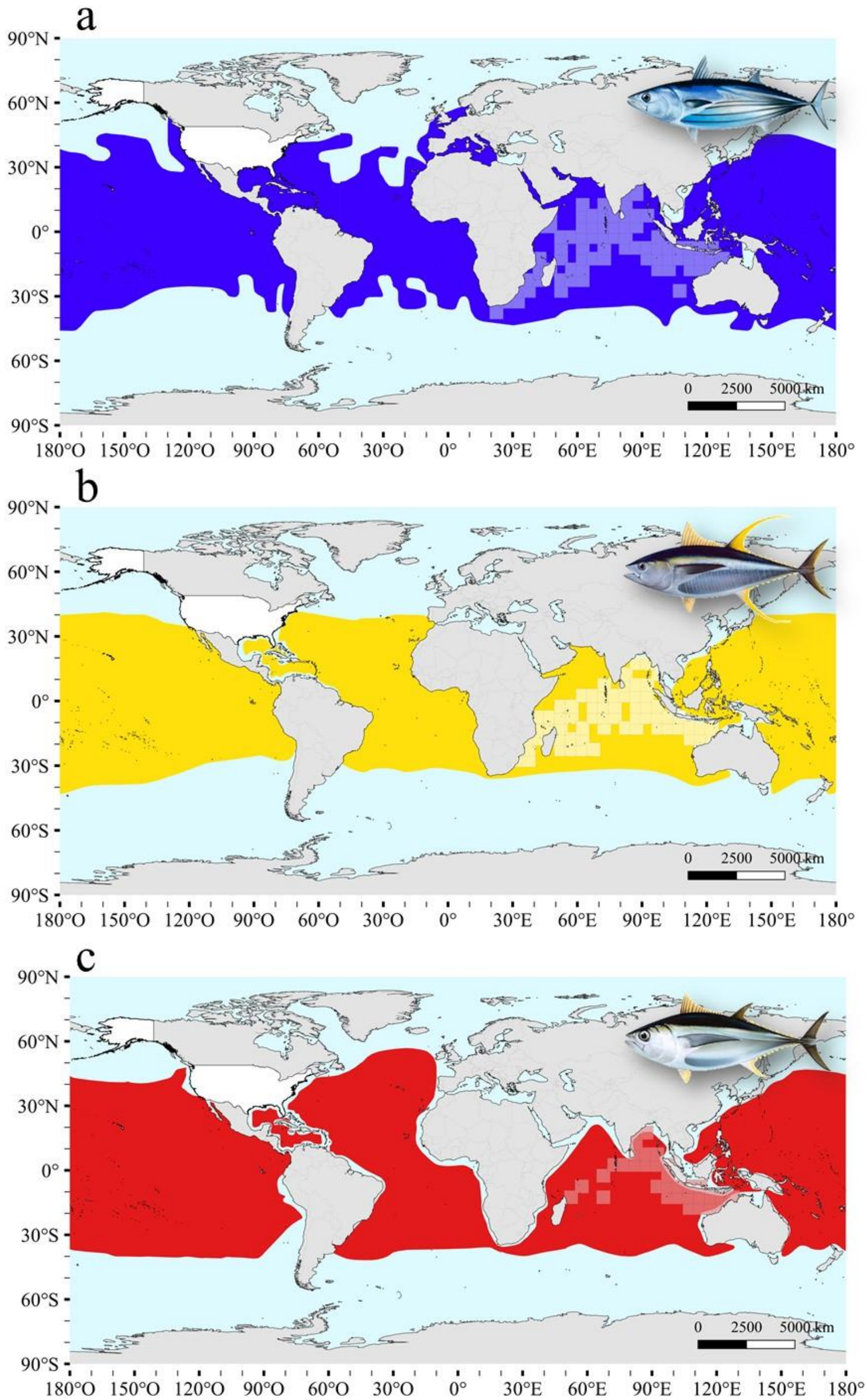

Figure 6. Potential habitat distribution range of (a) skipjack tuna *Katsuwonus pelamis*, (b) yellowfin tuna, *Thunnus albacares*, and (c) bigeye tuna, *Thunnus obesus*. Lighter squares represent the presence of larvae (*based on Reglero et al. 2014*). Distribution range was obtained from the IUCN Red List Spatial Data of tunas and billfishes version 5.2 (available at: https://www.iucnredlist.org/resources/spatial-data-download). Tuna images: IOTC © 2020.

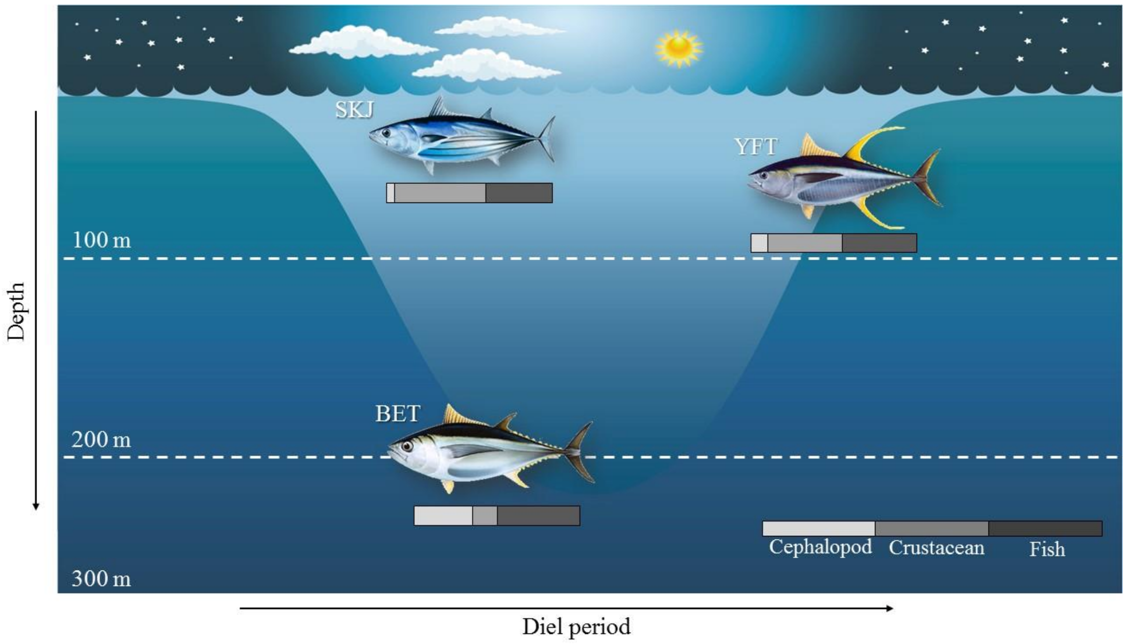

Figure 7. Trophic niche partitioning of adult tropical tuna in the western Indian Ocean: SKJ, skipjack tuna, *Katsuwonus pelamis*; YFT, yellowfin tuna, *Thunnus albacares*; BET, bigeye tuna, *Thunnus obesus*. Bars represent the importance of the main prey categories, squid (light grey), crustacean (mid grey) or fish (dark grey), in the diet of each predator (percent of the reconstituted weight). Adapted from Olson et al. (2016). Tuna images: IOTC © 2020.

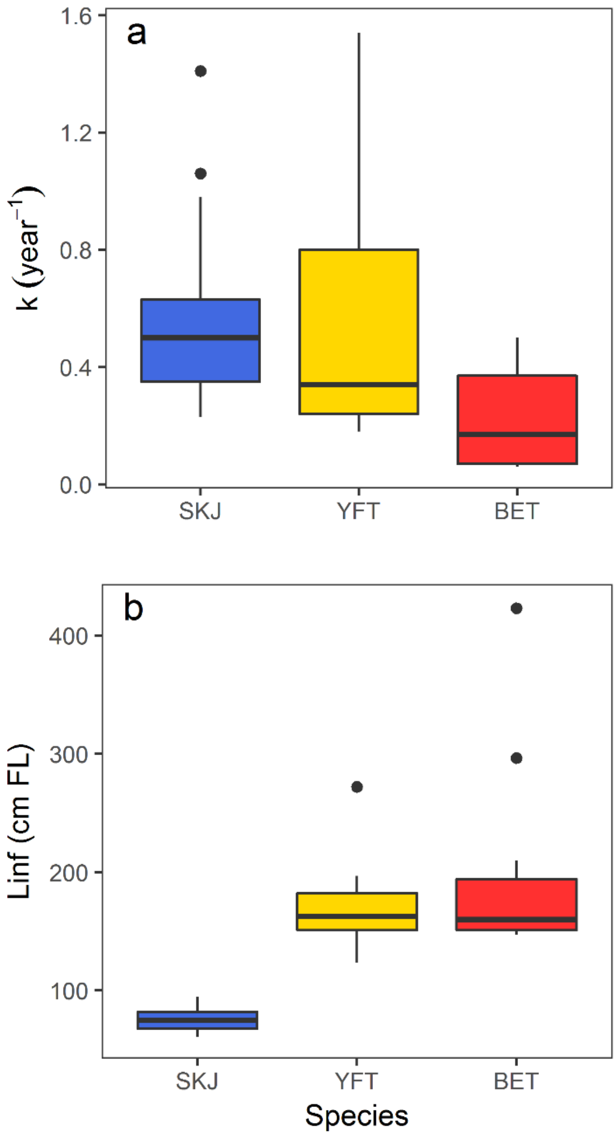

Figure 8. Comparison of reported growth rate coefficients (k) and asymptotic fork lengths (L_{∞}) for skipjack (blue), yellowfin (yellow) and bigeye (red) tuna in the Indian Ocean. Growth parameters have been obtained from Murua et al., 2017 supplementary material tables 10S, 13S and 16S.

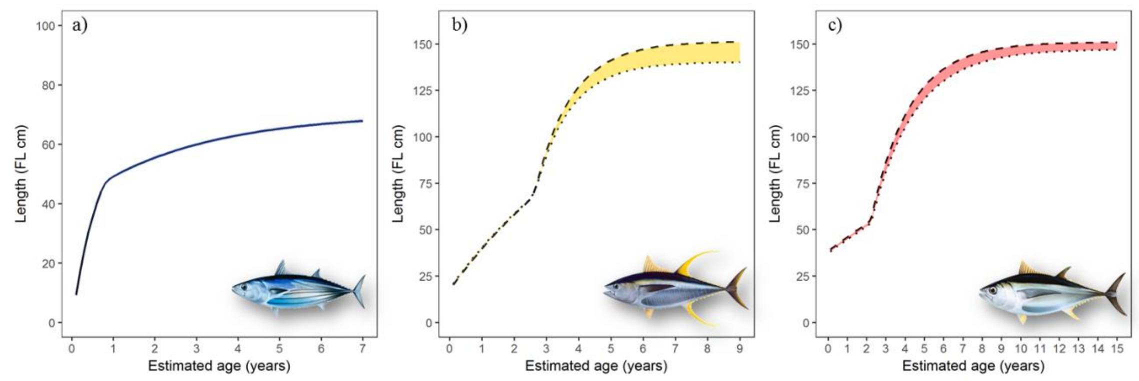

Figure 9. VB log K growth curves for (a) skipjack *Katsuwonus pelamis*, (b) yellowfin, *Thunnus albacares*, and (c) bigeye tuna, *Thunnus obesus* in the Indian Ocean after following (Eveson et al., 2015). In the case of yellowfin and bigeye tuna, growth is sex-specific, represented with a longdashed lines in males and with dotted lines in females. Tuna images: IOTC © 2020.

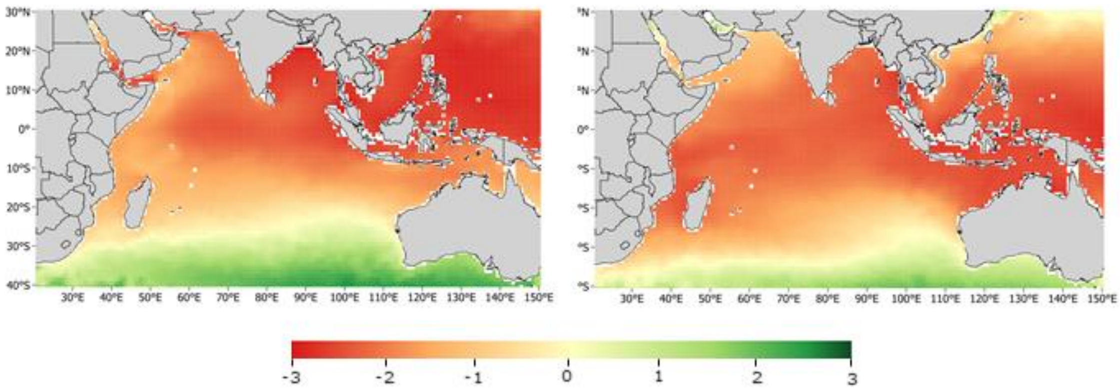

Figure 10. Predicted spatial variations in isotopic composition of oxygen in otoliths ($\delta^{18}O_{oto}$) following Trueman and MacKenzie (2012) and based on global surface water (0-50 m) measured $\delta^{18}O_{w}$ values (LeGrande and Schmidt, 2006), and parameters γ and β from Kitagawa et al., (2013). Maps are differentiated for summer monsoon (Jun-Sept 2017) and winter monsoon (Dec-Apr 2016-2017). Monthly data of Sea Surface Temperature (SST, ºC) was obtained from the "global-reanalysis-phy-001-031-grepv2-montlhy" dataset available in the EU Copernicus Marine Service Information (avaible at: https://marine.copernicus.eu/). Note that this simplistic model assumes constant parameters for the otolith fractionation equation and is based on coupled measurements of $\delta^{18}O_{w}$ values and SST at a spatial resolution of 1×1° grid.

Table 1. Summary of studies on Indian Ocean tropical tuna spawning seasonality. SKJ; skipjack tuna, *Katsuwonus pelamis*, YFT; yellowfin tuna, *Thunnus albacares*, and BET; bigeye tuna, *Thunnus obesus*. When two spawning seasons have been described in the same study 1; Main spawning season and 2; Secondary spawning season.

	Region	Spawning season	Source
SKJ	Western Indian Ocean	Year- round, but peaks of activity between November-March and June-July	(Stéquert et al. 2001)
SKJ	Western Indian Ocean	Year-round, but peaks of activity between November-March and June-July	(Grande et al. 2014)
SKJ	Indian waters	Year-round, peak of activity between December-March and a minor one from June to August	(Koya et al. 2012)
YFT	Central Indian Ocean, south Seychelles, west Sumatra Sri Lanka North Madagascar, north Australia	January to March 1: January to March, 2: April to June 2: October to December	(Stéquert and Marsac 1989)
YFT	Western Indian Ocean	November to April	(Hassani and Stéquert 1991)
YFT	Seychelles EEZ	November to February	(Majid and Ahmed 1991)
YFT	Pooled data for the Indian EEZ	January to April/May	(John and Sudarsan 1993)
YFT	Andaman Sea	November to April	(John 1995)
YFT	Bay of Bengal	November to April	(John et al. 1998)

YFT	North Arabian Sea	December to June	(Govindraj et al. 2000)
YFT	Western Indian Ocean	1: November to March, 2: June to August	(Stéquert et al. 2001)
YFT	Eastern Indian Ocean	November to April	(Nootmorn et al. 2005)
YFT	West Central Indian Ocean	January to June	(Zhu et al. 2008)
YFT	Western Indian Ocean	1: November to February, 2: June	(Zudaire et al. 2013)
YFT	Equatorial Area (0-10ºS)	December to March	(IOTC 2017a)
BET	Indian Ocean	January to March	(Solovieff 1970)
BET	Eastern Indian Ocean	October to January	(Ye et al. 2003)
BET	Southern Central Indian Ocean	October to January	(Li et al. 2010)
BET	Indian Ocean Eastern Indian Ocean	1: December to January 2: June	(IOTC 2017b)
BET	Western Indian Ocean	January to March	(Zudaire et al. 2016)