Longtail tuna, Thunnus tonggol *(Bleeker, 1851): a global review of population dynamics, ecology, fisheries, and considerations for future conservation and management*

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REVIEWS

Longtail tuna, *Thunnus tonggol* (Bleeker, 1851): a global review of population dynamics, ecology, fisheries, and considerations for future conservation and management

Shane P. Griffiths · **Duncan Leadbitter** · **Demian Willette** · **Farhad Kaymaram** · **Mohammed Moazzam**

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Abstract Longtail tuna (*Thunnus tonggol*) is a neritic species that supports commercial, artisanal and recreational fisheries throughout the Indo-Pacific region. Historically receiving little attention by commercial fisheries, the global annual catch of longtail tuna has steadily risen from around 30,000 t in the early 1980s to exceeding 200,000 t since 2004, reaching a peak of 291,264 t in 2007, and was 281,613 t in 2017. Catches of longtail tuna in the Indian Ocean now exceed catches of principal commercial target species, such as albacore and bigeye tunas. A sequence of stock assessments undertaken throughout the species' range since the late 1980s persistently indicated that at least three of the four stocks defined in this paper are likely to have been, and most likely are currently, subject to overfishing and overfished as a result of excess fishing effort on this relatively slow-growing and long-lived tuna species. As the spawning biomass of principal tuna target species continue to decline in both the Indian and western and central Pacific Oceans, the increasing catches of longtail tuna, other neritic tunas, and seerfishes is worrisome. Few conservation and management measures (CMMs) are currently in place specifically for longtail tuna, although in recent years some coastal States, Regional Fishery Bodies, and tuna Regional Fisheries Management Organisations have begun to develop initiatives to improve the catch and biological data quality for longtail tuna and sympatric species of neritic tunas and tuna-like species. This paper provides a global review of biological, ecological and fishery information to provide researchers, fishery managers and policy makers with the most current information from which to begin to guide future stock assessment and the development of CMMs for longtail tuna.

Keywords Coastal · Neritic · Northern bluefin tuna · Indo-Pacific

S. P. Griffiths (✉)
Inter-American Tropical Tuna Commission, 8901 La Jolla Shores Drive, La Jolla, CA, USA
e-mail: sgriffiths@iattc.org

D. Leadbitter
Australian National Centre for Ocean Resources and Security, University of Wollongong, Wollongong, NSW 2522, Australia

D. Willette
Biology Department, Loyola Marymount University, 1 LMU Drive, Los Angeles, CA, USA

F. Kaymaram
Iranian Fisheries Research Science Institute, Tehran, Iran

M. Moazzam
WWF-Pakistan, 46-K, PECHS Block 6, Karachi 75400, Pakistan

Introduction

The genus *Thunnus* within the Scombridae family includes eight species of tunas, some of which support among the largest and most economically important fisheries in the world. In 2017, the total reported global tuna catch of 5.4 million metric tonnes (t) constituted 7.9% of the world's total marine finfish catch of 67.9 million t (FAO 2019). As the global demand for seafood and animal protein is likely to continue to increase to support an estimated global human population of around 9 billion by 2050 (Msangi et al. 2013), tuna fisheries are likely to concomitantly increase pressure on the populations of target species, but also other edible or marketable species caught incidentally. Increasing removals of these high trophic level predators has the potential to initiate imbalances in trophic pathways that may eventually generate far-reaching impacts on the structure and functionality of marine ecosystems (Daskalov 2002; Polovina et al. 2009; Griffiths et al. 2019a).

One such species that has appeared to have become an increasing target, or at least an increasingly utilised incidental catch, of artisanal and small- and large-scale commercial tuna fisheries is the longtail tuna, *Thunnus tonggol* (Bleeker, 1851), which is the second smallest *Thunnus* species and found throughout tropical and subtropical neritic waters of the Indo-Pacific region (Froese and Pauly 2017). Longtail tuna has apparently avoided significant attention by industrial fisheries for several reasons. First, this species nearly exclusively occupies neritic areas close to landmasses and is rarely found beyond continental shelf waters where other tunas can be caught simultaneously (Yesaki 1994). Second, the species is small in size (often < 60 cm fork length) relative to other economically-important species of oceanic tunas and tends not to form large dense schools that are conducive for capture in commercial quantities by purse-seine or pole-and-line, and fish often dive when approached by vessels (Yesaki 1994).

However, due to their neritic distribution, longtail tuna are exploited by small-scale commercial and artisanal multi-species fisheries in many developed and developing countries throughout the Indo-Pacific and northwestern Indian Ocean that target neritic tunas including kawakawa (*Euthynnus affinis*), frigate and bullet tunas (*Auxis thazard* and *A. rochei*) and seerfishes (*Scomberomorous* spp.) (Yesaki 1994). Due to the often-poor reporting of neritic tunas in some countries, available landings data and perceived fishing impacts on the species are likely to be underestimated. Furthermore, because longtail tuna has not been considered a principal target species by the Indian Ocean Tuna Commission (IOTC), and has only recently been covered by the Regional Plan of Action on Neritic Tunas in South East Asia, the species has attracted little fundamental research regarding their biology, stock structure, movements or extent of fishery exploitation.

Previous reviews of the biology and fisheries of longtail tuna were conducted more than two decades ago (Jones 1963; Yesaki 1987, 1994), which warned fishery managers of rapidly increasing catches and a paucity of biological data from which population status assessments could be made to develop appropriate conservation and management measures (CMMs). Since those reviews, reported catches of longtail tuna have steadily increased—as have several other small sympatric species of neritic tunas that support many inshore fisheries of developing countries—with the annual global catch almost tripling from 105,910 t in 1993 to a peak of 291,264 t in 2007 and continuing at over 208,000 t annually to 281,613 t in 2017 (FAO 2019).

In the Indian Ocean in particular, between 1992–2012 longtail tuna catches increased four-fold from 40,580 to 170,221 t. Longtail tuna is now the fifth most important species in Indian Ocean tuna fisheries, with the 2017 catch of 144,747 t far exceeding catches of principal commercial tuna species including bigeye tuna (*Thunnus obesus*) (91,078 t) and albacore (*Thunnus alalunga*) (38,841 t) and constituting 8.9% of the total catch of tunas and seerfishes (Fig. 1a). The most important tuna species in Indian Ocean tuna fisheries are skipjack (*Katsuwonis pelamis*) (496,600 t in 2017) and yellowfin tuna (*Thunnus albacares*) (416,974 t) but a persistent decline in standardised longline catch per unit effort (CPUE) and spawning biomass of yellowfin tuna over the past decade has resulted in the stock being subject to overfishing and overfished for at least the last 3 years (Langley 2016b). Tuna fishing fleets in the Indian Ocean are therefore beginning to retain other species, such as neritic tunas and seerfishes, presumably to improve food security and service the nutritional needs of the large and rapidly-growing human populations in developing countries such as India, Iran and Pakistan (Crist et al. 2017; Techera 2018).

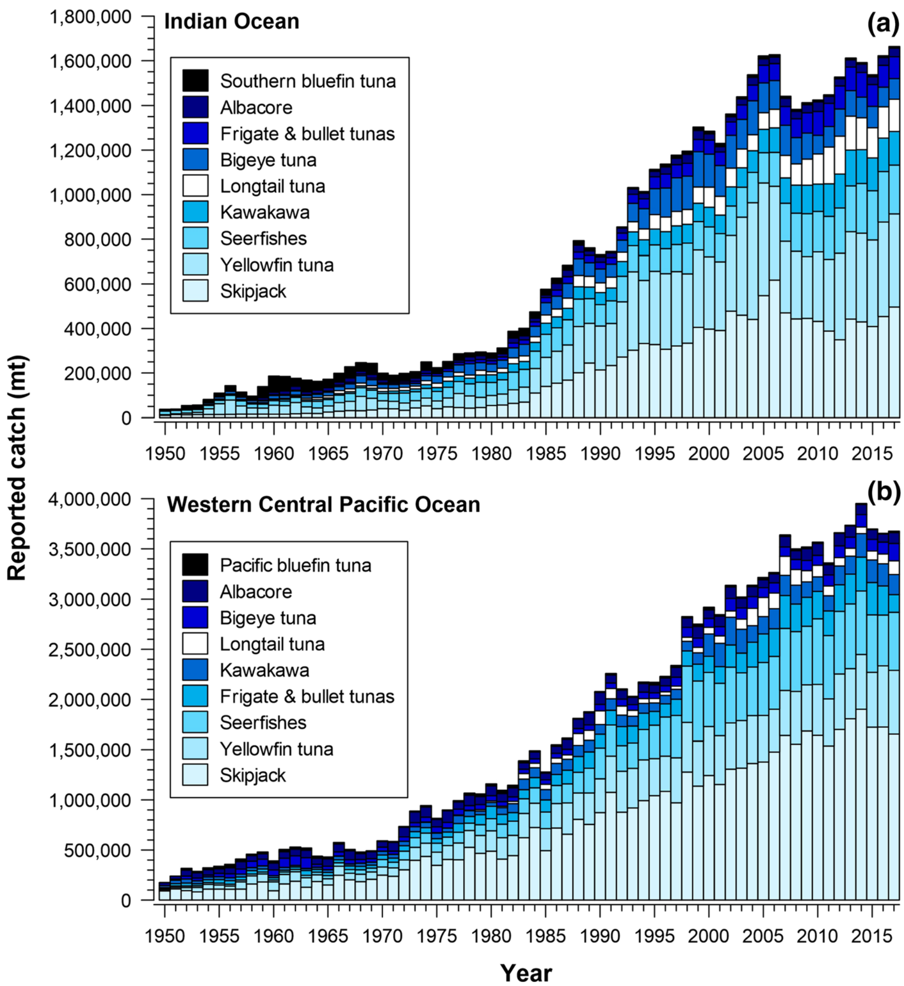

Fig. 1 Annual reported catches of tunas and seerfishes in **a)** the Indian Ocean (FAO Area 61 and 71) and **b)** the western and central Pacific Ocean (FAO Area 51 and 57) for 1950–2017 (Data source: FAO 2019). Longtail tuna catches are shown in white

In the Western and Central Pacific Ocean (WCPO), longtail tuna is the seventh most important tuna species, although the 136,866 t reported in 2017 comprised only 3.7% of the total catch of tunas and seerfishes due to the larger catches of skipjack (1,654,308 t), yellowfin tuna (635,483 t) and seerfishes (580,013 t) compared to the Indian Ocean (Fig. 1b).

In the Food and Agriculture Organisation of the United Nations' (FAO) 2011 review of the state of the world marine fishery resources, Majkowski et al. (2011) raised concerns over the increasing exploitation of neritic tunas and explicitly highlighted that "Longtail tuna (*T. tonggol*) is becoming increasingly important for canning and the object of substantial international trade." Coincidentally in the same year, the Indian Ocean Tuna Commission (IOTC) established the Working Party on Neritic Tunas (WPNT) to formally recognise the information needs to better manage neritic tunas and tuna-like species in the Indian Ocean, which longtail tuna has since been identified as a priority species by the WPNT (IOTC 2012). This recognition was also reflected in the South China Sea where growing concerns resulted in the development of a Regional Plan of Action for Sustainable Utilization of Neritic Tunas (RPOA-Neritic Tunas) in 2015 (SEAFDEC 2017).

Given the rapidly increasing catches of longtail tuna and need for reliable information to facilitate stock assessment and guide management and policy development in several regions throughout the Indo-Pacific region, the aim of this paper is to provide a comprehensive global review of the biology, ecology, population dynamics, and fisheries for longtail tuna and identify key knowledge gaps that are essential to being filled before the status of longtail tuna stocks can be reliably determined through stock assessment or their inclusion in ecosystem models that may be increasing used to facilitate emerging initiatives worldwide to implement ecosystem approaches to fisheries management.

Methods

Literature relating to longtail tuna was derived from a wide range of sources including scientific journal abstracts databases (e.g. Aquatic Sciences and Fisheries Abstracts), Web of Science, Google Scholar, individual university and scientific journal websites, the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and Inter-American Tropical Tuna Commission (IATTC) libraries, and the websites of Regional Fishery Bodies (RFBs), RFMOs, and the FAO. Reasonably little information on longtail tuna has been published in the peer-reviewed literature, so many citations in this review are unpublished reports and other forms of 'grey literature', theses, and conference, workshop and working group proceedings of reliable scientific sources such as IOTC's WPNT and the Southeast Asian Fisheries Development Center (SEAFDEC) member countries that are involved in the RPOA-Neritic Tunas.

Fisheries statistics summarised in this paper were taken from official FAO capture production statistics using FAO's freely available software "FishStatJ" (www.fao.org/fishery/statistics/software/fishstatj/en) that was released in November 2019, publicly available data by the IOTC published in each year of the WPNT website (http://www.iotc.org/science/wp/working-party-neritic-tunas-wpnt), and SEAFDEC through their online statistical bulletins (http://map.seafdec.org/fisherybulletin/). For catch statistics, the Indian Ocean included Major Fishing Areas 51 and 57, while the WCPO included Major Fishing Areas 61 and 71. All references to fish lengths in this paper are provided as fork length (FL), unless otherwise noted.

Unpublished tagging data for longtail tuna was provided by Australia's New South Wales Department of Primary Industries Game Fish Tagging Program (NSW GTP) (NSW DPI 2007).

Taxonomic description and evolutionary biology

Longtail tuna is the second smallest of eight *Thunnus* species and grows to a maximum recorded size of 145.2 cm total length (TL) (Al-Mamari et al. 2014) and 35.9 kg (Froese and Pauly 2017). It has a robust anterior tapering to an elongated posterior, hence its common name of "longtail". The first dorsal fin is similar to, or slightly smaller than, the second dorsal fin. The pectoral fins are long (22–31% of fork length) in fish < 60 cm and proportionally smaller (16–22%) in larger fish (Collette and Nauen 1983). Longtail tuna is the only species of the *Thunnus* genus that lacks a swim bladder as adults (Serventy 1942b). The ventral surface of the liver lacks striations (as for yellowfin tuna, *T. albacares*) and the first gill arch has 19–27 rakers (Collette and Nauen 1983).

Body colouration ranges from black on the back to dark blue above the lateral line with an iridescent blue band extending along the lateral line from the top margin of the gills to the caudal keel. The flanks are silver, grading to a silvery-white belly with opaque horizontal rows of elongated oval spots, which are often absent in larger fish. The first dorsal fin ranges from dark blue to pale yellow, while the second dorsal and anal fins are silvery-white to pale yellow. The finlets are pale yellow with grey to black margins. The tail is black to dark blue, occasionally with a pale-yellow colouration at the posterior base of the fork. The caudal keel is black to dark blue—as opposed to bright yellow in southern bluefin tuna, *Thunnus maccoyii*.

Despite the economic and ecological importance of *Thunnus* species, the evolutionary history of the genus has been poorly understood until recently; information that can be helpful for management and traceability efforts. Using morphological characteristics, Collette et al. (2001) partitioned these eight tuna species into two subgenera, the temperate *Thunnus* (bluefin group) containing *T. alalunga*, *T. obesus*, *T. thynnus*, *T. orientalis*, and *T. maccoyii*, and the tropical *Neothunnus* (yellowfin group) containing *T. albacares*, *T. atlanticus*, and *T. tonggol*. This partitioning is reflective of the geographic distribution of the two groups and being endothermic. More so, members of the bluefin group share the presence of additional visceral and cranial heat-exchanger systems (retia mirabilia) that heat the brain, eyes and viscera to optimise foraging and digestion, a feature lacking in the yellowfin group. Ciezarek et al. (2018) found this evolution of *Thunnus* endothermy to be associated with parallel selection and went on to use transcriptomics to infer the eight *Thunnus* are genetically distinct species. These results are in contrast to earlier exploration of the evolutionary relationship among *Thunnus* species which challenged the two-subgenera organization. Chow et al. (2006) used the rDNA first internal transcribed spacer (ITS1) to identify mitochondrial introgression among *Thunnus* species and found almost identical ITS1 sequences between members of the putative *Thunnus* and *Neothunnus* subgroups. These data inferred a largely unresolved phylogeny for *Thunnus*, a conclusion also found in sequences from mitochondrial Cytochrome oxidase I (COI) (Mudumala et al. 2011), and Control Region D-loop (Kumar et al. 2016) gene regions. Recently an evolutionary tree for *Thunnus* was derived using 128 genome-wide nuclear markers resulting in the repositioning *T. obesus* from the bluefin group to within the yellowfin group, further challenging the two-subgenera organization (Díaz-Arce et al. 2016). Due to its unique evolutionary and morphological traits, Gibbs and Collette (1967) had long ago positioned *T. obesus* as an intermediate of the bluefin and yellowfin groups. The more recent application of molecular tools has since better resolved the relationship among the *Thunnus* as a single monophyletic groups inclusive of eight distinct species (Díaz-Arce et al. 2016; Ciezarek et al. 2018).

Common and marketing names

Longtail tuna is known by several common, local and marketing names, often depending on how the meat is prepared for human consumption. The official FAO common names are longtail tuna (English), Thon mignon (French) and Atún tongol (Spanish). In Japan, longtail tuna is known as “Koshinaga”, while in its sashimi form it is “Koshinaga maguro”. In Malaysia the species is known as “Aya”, “Kayu”, or “Tongkol hitam”, in Indonesia it is known as “Tongkol abu abu” or “Fufu/Ikan asar”, while in the Philippines it's known as “Tambakol” or “Tonggol”. Similarly, in some Middle Eastern countries such as the United Arab Emirates, longtail tuna is also known as “Tonggol”, while in Iran it is known as “Havoor” (Hedayatifard 2011) and along the Pakistan coast it is known as “Dawan” and “Ahur” in the languages of Sindh and Balochi, respectively.

In Australia, longtail tuna was, and in many regions still is, called “Northern bluefin tuna”, especially in the recreational fishery. This has caused confusion with Pacific bluefin tuna (*T. orientalis*) that was long considered a subspecies (*T. thynnus orientalis*) of Atlantic bluefin tuna (*T. thynnus*). Collectively, the latter two species were officially known as “Northern bluefin tuna” before being separated into two species based on morphology (Collette 1999) and genetics (Tseng et al. 2011). In fact, a major Australian-owned cannery appeared to capitalise on the ambiguity in nomenclature and marketed longtail tuna as northern bluefin tuna that serendipitously implied the product was premium sashimi grade *T. orientalis*. This continued until at least 2002 until the issue was resolved by the Australian Advertising Standards Bureau (ASB 2002).

Geographic range

Longtail tuna inhabit tropical and subtropical waters of the Indo-Pacific region 47° N–37° S and 32° E–154° E (Fig. 2). On the easternmost side of their distribution the species can be found as far north as the northeastern Sea of Japan and throughout the southern Yellow Sea to China and South Korea (Yoon et al. 2013) and as far south as Twofold Bay in southeastern Australia (Serventy 1942b). On the western side, their distribution extends from northwestern Arabian Sea—including the Gulf of Oman, and Persian Gulf, the Red Sea—and southward to the Maputo Province in southern Mozambique (Chacate and Mutombene 2014). Their distribution also includes the Comoros archipelago (Mohamed Toihir 2018) and Madagascar (Fanazava 2015). In many parts of their distribution, the geographic range of longtail tuna varies seasonally. For example, along Australia's east coast when the warm waters of the East Australian Current (EAC) are at their most southerly extent during the Austral summer and autumn longtail tuna can be found over 1000 km south of their usual distribution (Serventy 1942b). In the South China Sea, commercial catches and tagging data suggests that the distribution of longtail tuna moves northward during the northeast monsoon season, and southward to coastal regions for the remainder of the year (Raja Bidin 2002).

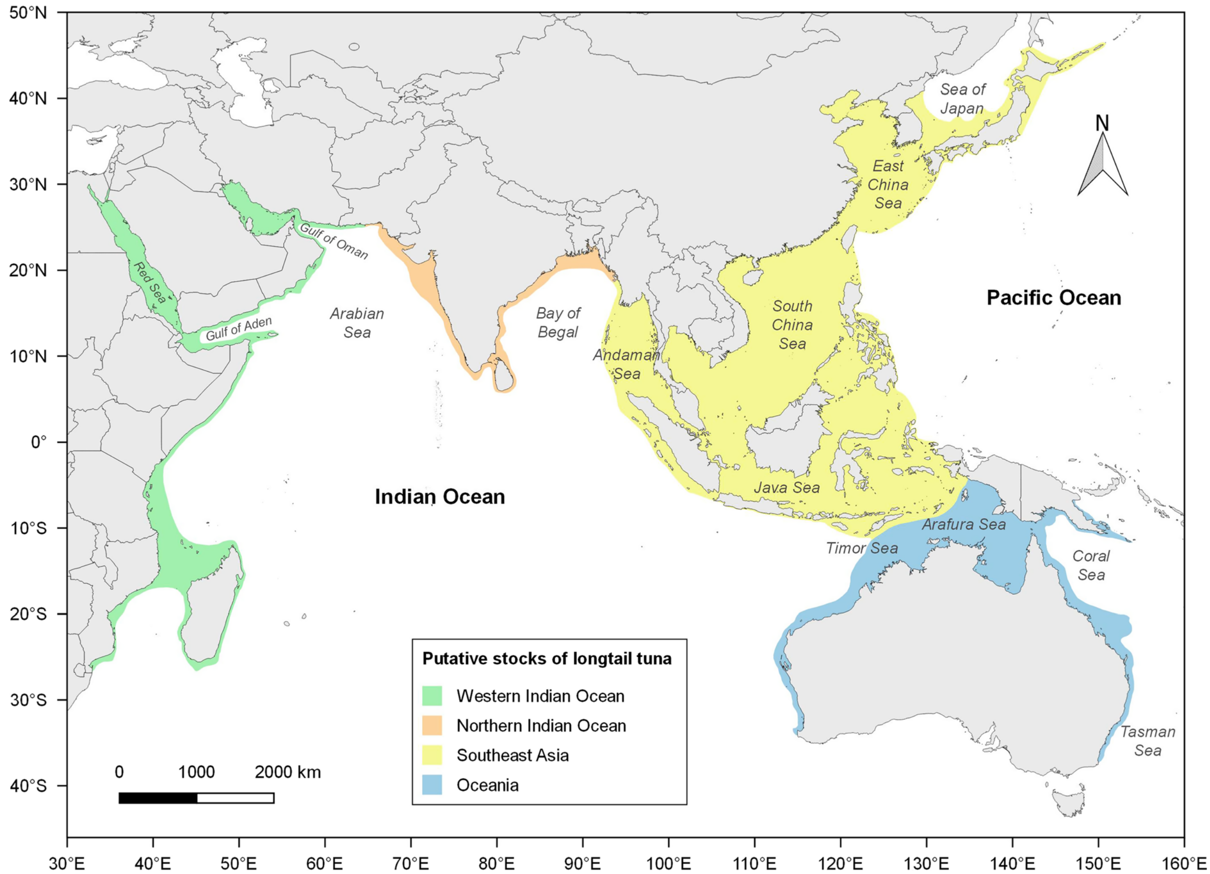

Fig. 2 Map showing the worldwide distribution of longtail tuna and the four putative stocks based on best-available information from genetic, morphometric and tagging studies

Within their broad geographic range, longtail tuna have quite a unique distribution compared to other *Thunnus* species in that they nearly exclusively occupy the neritic regime close to landmasses and are rarely found far offshore (Yesaki 1994). They also tend to avoid areas near the mouths of large estuaries during periods of rainfall where waters have low salinity and/or high turbidity (Collette and Nauen 1983). Although they occupy shallow neritic waters, longtail tuna tagged with electronic tags have occupied depths of at least 90 m (Griffiths 2011). Therefore, in constructing the geographic distribution of longtail tuna (Fig. 2), we confined its distribution from the coast out to the 200 m isobath—based on best available depth preferences (see "Habitat specificity and movement")—and extended the depth distribution to incorporate reliable occurrence records.

Stock structure

There is great uncertainty regarding the stock structure of longtail tuna throughout their range. Serventy (1956) was one of the first researchers to explore stock structure of longtail tuna and suggested that separate stocks—and possibly even two subspecies—may exist in Australian waters based on the distinct difference in gill raker counts and size distributions of fish present off the eastern, northern and western coasts of Australia. Wilson (1981a) tested this hypothesis by using morphometrics and allozyme electrophoresis and found no differences between samples collected from Papua New Guinea, Gulf of Carpentaria, Moreton Bay (Queensland) and Shark Bay (Western Australia). However, he warned that the results need to be viewed with caution owing to small sample sizes from the latter three locations.

Abdulhaleem (1989) found significant differences in the number of gill rakers in fish sampled from the waters off Oman and the southeastern coast of India and suggests that this may be indicative of at least two separate stocks in the Indian Ocean.

Molecular markers have been widely used to delineate genetic stocks of marine fishes including tuna, albeit data being limited for smaller species like longtail tuna. A review of tuna population structure literature identified 50 genetically distinct tuna populations worldwide, with two populations inferred for longtail tuna (Kumar and Kocour 2015). Two recent studies used advance mitochondrial DNA (mtDNA) displacement loop (D-loop) region genetic analyses to explore stock structure of longtail tuna in the northern hemisphere. Kunal et al. (2014) sampled from two regions in northwest Indian waters and found no significant genetic differentiation, suggesting a single stock throughout Indian waters. Willette et al. (2016) used similar mtDNA D-loop analysis on samples collected from Indonesia, Vietnam, and the Philippines to conclude that longtail tuna exist as a single stock within the South China Sea. They compared their sequences with those of Kunal et al. (2014) and found statistically significant genetic differentiation, indicating that fish from the South China Sea and Indian waters comprise two distinct stocks.

It is clear from length-frequency data reported in studies throughout the distribution of longtail tuna, that there is an increase in fish size with increasing latitude. This appears to be most apparent in Australian waters, where several studies (Serventy 1942b, 1956; Wilson 1981a; Stevens and Davenport 1991; Griffiths 2010; Griffiths et al. 2010a) have shown fish to be smallest in the Timor and Arafura Seas in northern Australia and gradually increasing in size with increasing latitude southward along both the east and west coasts. Very few small fish less than 40 cm have been recorded from Australian waters, whereas fish of this size are abundant throughout Southeast Asia and support large commercial and artisanal fisheries. This suggests that there may be a southward ontogenetic migration from a northern nursery ground, such as the South China Sea (see "Reproductive biology"). As a result, longtail tuna may exist as a single stock throughout Southeast Asia and Oceania. However, considering the significant geographic and oceanographic barriers evident throughout this region, such as the complex of islands throughout the Savu and Banda Seas and the Sunda Trench that concentrates the strong Indonesian Throughflow current between northern Australian and Southeast Asian waters (Lee et al. 2002), the possibility of separate stocks of longtail tuna being present throughout its geographical range cannot be discounted. In the absence of large-scale tagging data and detailed genetic analyses throughout this region, the extent of mixing of fish between countries or water masses remains unknown.

Reproductive biology

Sex ratio

Longtail tuna is a gonochoristic species exhibiting no signs of sexual dimorphism in external morphology (Griffiths et al. 2019b). In the nine studies that have reported sex ratio (Table 1), there is little evidence of departure from the expected male:female ratio of 1:1 across the entire length range. Griffiths et al. (2010a) found a (2:1) bias towards males for large (> 100 cm FL) longtail tuna along the east coast of Australia but speculated this may be due to inadequate sampling of larger fish—due to their naturally lower proportion in the population—rather than a true departure from the 1:1 sex ratio they documented in smaller size classes. A similar sex ratio bias towards males has been noted for larger size classes of other *Thunnus* species (Hurley et al. 1981; Wild et al. 1995, Schaefer 1998; Gunn et al. 2008). It has been speculated a sex ratio bias towards males in large yellowfin tuna may be due to higher natural mortality in females as a result of higher energetic costs of gonad development and spawning (Schaefer 1998). In contrast, a study of 373 longtail tuna along the northwestern coast of India (Mohammed Koya et al. 2018) found a male:female ratio of 1:2.1, with the proportion of males declining with increasing size.

Maturity

Length-at-maturity has been estimated in only a few studies, with most reporting the length at first maturity (L_M) rather than the length at which 50% of the population is mature (L_{50}), which is a more conservative estimate of maturity and allows the development of maturity-at-length (or age) ogives that are generally

Table 1 Summary of parameters describing the reproduction dynamics of longtail tuna estimated in studies from around the world, including length-at-first-maturity (L_M), length-at-50% maturity (L_{50}) and batch fecundity based on histological staging (HIS), macroscopic staging (MAC), or a gonadosomatic index (GSI). Months defining the main spawning season in each study are shown

Country	Author	Gonad staging	Sex ratio M:F	Length type	Female maturity L_M	Female maturity L_{50}	Batch fecundity: Fecundity range	Batch fecundity: Mean fecundity	Spawning season
Oceania									
Australia	Serventy (1956)	MAC	–	FL	51.0	–	–	–	Sept–Oct
Australia	Griffiths et al. (2019b)	HIS	1:1.3	FL	52.7	53.5	600,215–3,468,350	1,516,680 (± SD 743,980)	Sept–Mar
Papua New Guinea	Wilson (1981a)	MAC	1:1	FL	60.0	–	768,000–1,900,000	–	Sept–Feb
Southeast Asia									
Japan	Itoh et al. (1999)	GSI	1:0.88	–	–	–	–	–	May–Sept
Taiwan	Chiang et al. (2011)	HIS	1:1.18	FL	37.0	–	–	–	Nov–Dec
Thailand	Chiampreecha (1978)	MAC	–	–	>47.0	–	–	–	–
Thailand	Klinmuang (1978)	MAC	1:1	–	45–50	–	1,200,000–1,900,000	1,400,000	–
Thailand	Yesaki (1982)	MAC	1:1	–	40.0	43.0	–	–	–
Thailand	Cheunpan (1984)	MAC	–	–	34.2	39.6	–	–	–
Thailand (Gulf)	Hassadee et al. (2014)	MAC	1:0.97	FL	28.8	42.2	99,773–3,165,849	1,438,583 (± SD 920,715)	Feb–Aug
Thailand (Andaman)	Hassadee et al. (2014)	MAC	1:0.76	FL	41.0	44.0	44,628–240,477	123,966 (± SD 55,470)	April
Malaysia	Raja Bidin and Rumpet (1990)	GSI	–	–	47.8	–	–	–	May–Aug
Indonesia	Hidayat and Noegroho (2018)	MAC	1:0.77	FL	41.1	–	–	–	May–Aug
Indonesia	Wagiyo and Febrianti (2015)	MAC	1:0.85	FL	38.9	–	–	–	Apr–May
Eastern Indian Ocean									
India	Abdussamad et al. (2012)	MAC	–	FL	48.0	51.1	227,364–1,092,891	–	–
India	Mohammed Koya et al. (2018)	MAC	1:2.11	TL	48.0	60.7	–	–	Dec–Apr

preferred for stock assessment. Again, the lack of studies that have estimated L_{50} is most likely due to insufficient sampling across the entire size spectrum of the stock, particularly large fish, which is important when fitting logistic regression models to maturity-at-length data to estimate L_{50}. Furthermore, some studies estimated L_M using an arbitrary GSI threshold value to define maturity without histological validation (Cheunpan 1984; Raja Bidin and Rumpet 1990). Therefore, many reproductive studies have produced maturity estimates that are probably not representative of the wider population and should therefore be viewed with caution.

Nonetheless, there appears to be a large difference in L_M estimates for females between the northern and southern hemisphere, and between regions within each hemisphere (Table 1). In the northern hemisphere, only one study (Chiang et al. 2011), undertaken in Taiwan waters, described maturity based on histological examination of 231 ovaries. This study estimated L_M to be 37 cm but noted that L_{50} could not be reliably estimated as fish larger than 80 cm occur in Taiwanese waters since they are rarely caught in the commercial or artisanal fisheries from which samples were collected.

Eight studies conducted in the waters surrounding Thailand and Malaysia—including the Andaman Sea, Malacca Strait, the Gulf of Thailand and the south China Sea—used either a gonadosomatic index (GSI) or macroscopic staging of ovaries to derive L_M estimates of 28.8–44.0 cm (Table 1). No study used reliable histological methods, but three studies (Yesaki 1982; Cheunpan 1984; Hassadee et al. 2014) used macroscopic staging of ovaries to produce L_{50} estimates of 39.6–43.2 cm for the region.

Further west, studies using macroscopic staging of ovaries produced quite different L_M estimates of 48 cm for Indian waters (Abdussamad et al. 2012, Mohammed Koya et al. 2018) and L_{50} estimates of 51.1 cm TL and 60.7 cm FL, respectively.

In the southern hemisphere, three studies have examined the reproductive biology of longtail tuna using either macroscopic staging (Serventy 1956; Wilson 1981a) or histology (Griffiths et al. 2019b). Each study revealed that female longtail tuna mature at larger sizes than in the northern hemisphere (Table 1). In the waters of Australia and Papua New Guinea, macroscopic staging of ovaries by Wilson (1981a) led to the conclusion that fish first matured at 51 cm and 60 cm in each respective region. Using histological analysis of longtail tuna samples from northern and eastern Australia, Griffiths et al. (2019b) found the smallest mature female was 52.7 cm (2.3 years of age), while L_{50} and the age at 50% maturity (A_{50}) was estimated to be 53.6 (± 95% CI 46.3–57.0) cm and 2.51 (± 2.14–2.79) years, respectively. However, due to the small sample size of fish less than 50 cm, there is the potential for L_M and L_{50} to be overestimated.

Timing of spawning

Several studies have investigated the timing of spawning of longtail tuna in a number of countries, primarily using a GSI or macroscopic staging of gonads (Table 1). A common result from these studies is that spawning occurs over a period of several months during the warmest period of the year in each region. However, there is an apparent difference between the northern and southern hemisphere as to the seasons when spawning takes place.

Yesaki (1982) used macroscopic staging of ovaries to determine that fish in the waters off the west coast of Thailand spawned during two periods; at the beginning and end of the monsoonal period between January–April and August–September. Similarly, Cheunpan (1984) found two spawning peaks slightly later in the year between March–May and July–December in the Gulf of Thailand. Further south in the South China Sea, Hidayat and Noegroho (2018) macroscopically staged ovaries to determine fish spawned between May and August. At a similar latitude, Mohammed Koya et al. (2018) also used macroscopic staging of ovaries to determine longtail tuna spawned off the coast of India between December–April, with a possible second smaller spawning peak in June–September, although some mature fish were found year-round.

In the southern hemisphere, there appears to be only one spawning peak in the waters of Australia and Papua New Guinea, primarily during the spring and summer, although the spawning period slightly differed among studies. Serventy (1956) used macroscopic staging of ovaries to suggest a spawning period of September–October in southeastern Australia. Wilson (1981a) used macroscopic staging of ovaries and a GSI to determine longtail tuna had a protracted spawning season in Papua New Guinea between October and April. Similarly in northern and eastern Australia, Griffiths et al. (2019b) used histology and GSI to determine that longtail tuna have an extended spawning season between October and February.

Spawning locations

The specific spawning locations of longtail tuna is poorly understood throughout most of its range. However, based on the capture of ripe females and/

or the presence of larvae, possible spawning grounds have been proposed for the southern Andaman Sea (Puewkhao et al. 2000), the western Sea of Japan and the northern region of the East China Sea (Itoh et al. 1999, Yoon et al. 2013), and the outer neritic zone in the Gulf of Thailand (Yesaki 1982). Furthermore, the high proportion of juveniles < 20 cm in fishery catches in these regions (Yesaki 1982, 1989; Itoh et al. 1996) indicate they are nursery habitats and that spawning probably takes place nearby.

In Oceania, the evidence to identify spawning locations is less convincing. Wilson (1981a) hypothesised that spawning may take place in the vicinity of Aru Island in the northern Arafura Sea. This was based on the presence of smaller size classes of fish in this region, compared to the east coast of Australia, and elevated sea surface temperatures (24–28 °C) that are conducive for spawning among *Thunnus* species (Schaefer 2001). However, this spawning hypothesis is questionable since no ripe females were captured during 6 years of monthly sampling. Furthermore, the smallest fish recorded in his study was 46 cm—around 1–2 years of age—suggesting that these fish may have been spawned elsewhere and moved to the study region.

Along the southeastern coast of Australia Serventy (1956) observed longtail tuna having spent ovaries during April and suggested that fish most likely recently spawned further north—possibly in the vicinity of the Great Barrier Reef in the Coral Sea—before travelling southward with the seasonally expanding EAC that reaches its southernmost extent in around May each year (Ridgway and Godfrey 1997).

Recent histological analysis of longtail tuna ovaries provided conclusive evidence of at least three spawning locations in Australian waters (Griffiths et al. 2019b). In this study, monthly sampling was undertaken over a 15-month period across a large region incorporating the Timor, Arafura, Coral and Tasman Seas—including the Gulf of Carpentaria—to central New South Wales. Post-ovulatory follicles (POFs) were present in ovaries from fish caught in tropical waters in the western Arafura Sea, waters offshore of the Edward and Holroyd rivers in the eastern Gulf of Carpentaria, and in coastal waters inside the Great Barrier Reef along the central Queensland coast.

Although spawning was confirmed in these regions, the capture of only 8 fish containing POFs from a sample of 106 mature females suggests that the majority of longtail tuna may spawn elsewhere. It is possible they may move to offshore waters to spawn, which has been suggested to occur off Malaysia and Japan (Yesaki 1989; Itoh et al. 1999). In October–November 2015, twenty small (< 40 cm) longtail tuna were captured by a commercial fisher in waters of 100 m depth off Fraser Island, Queensland and fish of a similar size are reputed to occur at the location at a similar time each year (Dr Julian Pepperell, pers. comms.). Further studies are required to explore this issue, including larval and catch surveys in offshore waters during the spawning season, possibly in areas known to be spawning locations for other *Thunnus* species, such as the Coral Sea (McPherson 1991).

Batch fecundity

Only five studies have published fecundity estimates for longtail tuna (Table 1), all of which describe batch fecundity as opposed to total fecundity. In the southern hemisphere, Wilson (1981a) estimated female fish (75–98 cm) from Papua New Guinean waters produce 768,000–1,900,000 oocytes per spawning. However, he was unable to obtain samples of ripe females and therefore, these fecundity estimates are probably underestimates.

In eastern and northern Australian waters, Griffiths et al. (2019b) estimated the fecundity of 15 mature female fish (68.5–106.3 cm) with ripe ovaries (histological Stage V) to be 600,215–3,468,350 oocytes, with the average batch fecundity being 1,352,760 ($\pm$ SD 47,642) oocytes. This study also determined that there was a strong positive relationship between fecundity and fish length, indicating that larger females produce a higher number of oocytes. However, mean relative fecundity (163.25 $\pm$ SD 52.36) oocytes per gram of BW per spawning showed no relationship with fish length, implying that all spawning females, regardless of size, make a similar contribution to the oocyte production biomass.

In the northern hemisphere, Klinmuang (1978) examined the ovaries of four fish between 44–49 cm from the western Gulf of Thailand and off the east coast of Malaysia, and estimated batch fecundity to be between 1.2–1.9 million oocytes. In a more recent study in the same region, Hassadee et al. (2014) examined 14 fish (38.4–49.2 cm) and estimated fecundity to be 99,773–3,165,849 oocytes. However, this study found fecundity estimates to be lower (44,628–240,477 oocytes) in 12 fish (43.0–49.5 cm) sampled from the adjacent Andaman Sea.

To the west of the Andaman Sea in coastal Indian waters, Abdussamad et al. (2012) produced batch fecundity estimates of 227,364–1,092,891 oocytes for fish between 53.7–79.4 cm. However, the number and the histological stage of specimens used was not reported and therefore their results should be viewed with caution.

Age, growth and longevity

There are marked regional differences in maximum size of longtail tuna. For example, fish found throughout Southeast Asia from the Sea of Japan to the South China Sea appear to be smallest, with a maximum recorded length of 58 cm (Itoh et al. 1999, Mohri et al. 2010). The species then tends to attain a larger maximum size towards the western and southern boundaries of their distribution, with fish larger than 120 cm frequently recorded in the Gulf of Oman and the Persian Gulf (Prabhakar and Dudley 1989; Kaymaram et al. 2011), and along the southeastern coast of Australia (Serventy 1942a, 1956; Griffiths 2010, 2012).

A number of growth studies have been undertaken on longtail tuna although their entire geographic distribution, with the majority of studies undertaken in countries where significant commercial and/or artisanal fisheries exist for the species (e.g. Thailand, Malaysia, India, Iran and Oman). Tracing modal length progressions of cohorts over time using length-frequency data has been the primary method used to estimate growth of longtail tuna. These studies have generally relied on fishery dependent methods, such as market sampling or scientific observers onboard commercial vessels (Table 2). Unfortunately, length-frequency analyses can be an unreliable method for estimating growth parameters for use in fisheries stock assessment (Fournier et al. 1998). This is because the size selectivity of the fishing gear does not allow all cohorts present in the population to be properly represented in the sample through time, as cohorts grow in size. Consequently, growth rates are biased towards prominent size classes susceptible to capture by the gear. A further problem is if the collection of samples is not sufficiently frequent, cohorts of younger and faster growing fish may be missed in subsequent sampling events, leading to inaccurate growth parameters being estimated. Furthermore, even where the entire population is represented in samples, older cohorts begin to become increasing difficult to identify through time, as they begin to merge with other cohorts as their growth rate decreases and their relative abundance in the population declines.

Not surprisingly, the VBGF parameters (L_{∞}, K and t_0) estimated in studies analysing length-frequency data vary widely, even for studies conducted in the same region. For example, in the Gulf of Thailand, Supongpan and Saikliang (1987) estimated L_{∞} and K to be 58 cm and 1.44, respectively, implying that longtail tuna are fast-growing and short-lived, reaching 58 cm by age 5. In the same region, Yesaki (1989) estimated L_{∞} and K to be 108 cm and 0.55, respectively, suggesting the species is longer-lived, reaching 101 cm by age 5 (Table 2). It is likely that this variability is an artefact of size selectivity of the gear from which fish were sampled and the time periods when sampling was undertaken, as fish move seasonally through Southeast Asia (Raja Bidin and Rumpet 1990; Chiang et al. 2011).

Four studies aged longtail tuna using a more accurate method of quantifying growth increments in sagittal otoliths. These were undertaken in the Sea of Japan (Itoh et al. 1999), the Gulf of Oman (Brothers 1990), the waters from northern Australia to Papua New Guinea (Wilson 1981a), and the coastaal waters off the northern and eastern coasts of Australia (Griffiths et al. 2010a) (Table 2). The former three studies estimated age by counting presumed daily increments and suggested that longtail tuna are fast-growing and short-lived. Itoh et al. (1999) aged 33 small fish (12–49 cm), and estimated L_{∞} and maximum age as 55 cm and 434 days, respectively. Brothers (1990) aged only 22 fish (30–82 cm) and estimated L_{∞} to be 78.5 cm. In contrast, Wilson (1981a) aged 26 fish from a broader size range (45.3–110.9 cm), estimated an L_{∞} of 131.8 cm and concluded that the oldest fish was 1700 days (4.7 years) old at 110.9 cm. However, the results of these three studies should be viewed with caution. Apart from the small sample sizes, the growth model parameters would have been biased in each case since substantial components of the total size spectrum of the populations were not sampled.

Table 2 Summary of von Bertalanffy growth parameters, longevity and length-at-age (in cm) estimated in studies of longtail tuna where growth was characterised using otoliths or length-frequency (LF) analysis

Area	References	Ageing method	Length range (cm)	Sample size	von Bertalanffy growth parameters			Length-at-age			Longevity (years)
					L_∞	K (year^{-1})	t_0 (year^{-1})	1	3	5	
Oceania											
Australia	Serventy (1956)	LF	–	–	–	–	–	38	62	–	–
Australia	Griffiths et al. (2010a)	Otoliths	24–125 FL	461	135.4	0.233	− 0.020	27	66	91	18.7
Papua New Guinea	Wilson (1981a)	LF	46–103 FL	1477	122.91	0.410	− 0.032	42	87	107	–
Papua New Guinea	Wilson (1981a)	Otoliths	45–111 FL	26	131.8	0.395	− 0.035	44	92	114	4.7
Southeast Asia											
Japan	Itoh et al. (1999)	Otoliths	12–49 FL	33	55.0	1.700	− 0.089	46	54	55	1.2
Thailand	Chiampreecha (1978)	LF	–	–	–	–	–	27	45	–	–
Thailand	Klinmuang (1978)	LF	–	–	–	–	–	31	–	–	–
Thailand	Yesaki (1982)	LF	20–58	–	–	–	–	30	–	–	–
Thailand	Supongpan and Saikliang (1987)	LF	–	–	58.2	1.440	− 0.027	45	57	58	–
Thailand	Yesaki (1989)	LF	–	–	108.0	0.550	–	46	87	101	–
Malaysia	Chiampreecha (1978)	LF	–	–	–	–	–	30	–	–	–
Malaysia	Raja Bidin and Rumpet (1990)	LF	31–50	–	73.5	0.440	–	26	54	65	–
Indonesia	Wagiyo and Febrianti (2015)	LF	29–51	168	55.7	1.500	–	43	55	56	–
Indonesia	Restiangsih and Hidayat (2018)	LF	18–81	168	85.0	0.400	0.046	27	59	73	–
Eastern Indian Ocean											
India	Silas et al. (1986)	LF	–	–	93.0	0.490	− 0.240	42	74	86	–
India	James et al. (1993)	LF	16–92	–	94.0	0.480	–	36	72	85	–
India	Pillai et al. (2003)	LF	36–100	–	108	0.550	–	46	87	101	–
India	Ghosh et al. (2010)	LF	30–98	2976	107.4	0.180	− 0.073	19	46	64	–
India	Abdussamad et al. (2012)	LF	23–111 FL	–	123.5	0.510	− 0.032	51	97	113	4.5
India	Kumar et al. (2017)	LF	22–86	–	98.7	0.390	0.335	31	68	84	5.0
Western Indian Ocean											
Pakistan	Ahmed et al. (2016)	LF	–	300	69.9	0.934	− 0.09	45	66	69	–
Iran	Kaymaram et al. (2011)	LF	26–128	4313	133.7	0.350	–	40	87	111	–
Iran	Yasemi et al. (2017)	LF	27–107		111.2	0.300	− 0.380	38	71	89	–
Iran	Darvishi et al. (2018)	LF	25–124	4383	129.6	0.390	− 0.280	51	94	113	
Oman	Prabhakar and Dudley (1989)	LF	24–118	12333	133.6	0.228	–	27	66	91	–

Table 2 continued

Area	References	Ageing method	Length range (cm)	Sample size	von Bertalanffy growth parameters			Length-at-age			Longevity (years)
					L_∞	K (year^{-1})	t_0 (year^{-1})	1	3	5	
Oman	Brothers (1990)	Otoliths	30–82	22	78.5	0.679	− 0.490	50	71	77	7.0
Yemen	Anon (1989)	LF	–	–	104.0	0.250	–	23	55	74	–

In an attempt to resolve some of the sampling artefacts in previous ageing studies, Griffiths et al. (2010a) examined the otoliths from 497 fish (24–125 cm) and validated annual growth increments using daily ageing and edge type analysis. Their study estimated that longtail tuna live for at least 18 years and obtained a similar estimate of L_∞ (135.4 cm) as Wilson (1981a) from the adjacent waters of Papua New Guinea. However, their estimate of K (0.223 year^{-1}) was nearly half that of Wilson (1981a) (K = 0.395 year^{-1}), implying the species is slow-growing, and having comparable growth dynamics to bigeye tuna (*T. obesus*) and southern bluefin tuna (*T. maccoyii*), particularly in that these species live in excess of 18 years (Griffiths 2010). Earlier work by Prabhakar and Dudley (1989) in Omani waters who analysed length data for 300–500 fish collected every 10 days per month for nearly 2 years also suggested longtail tuna are relatively long-lived, reaching at least 10 years of age at around 116 cm. In a recent ageing study conducted in adjacent Irani waters, Darvishi et al. (2018) analysed monthly length-frequency samples (n = 4383) comprising a wide size range (25–124 cm) and also determined that longtail tuna are slow-growing and long-lived, possibly reaching 12 years of age.

Trophic ecology

Diet composition

Longtail tuna plays an important role as both a predator and as prey in coastal ecosystems. Although relatively few studies have quantified the diet composition of longtail tuna, available data indicates they are an opportunistic predator consuming a wide range of prey types.

In the Gulf of Mannar—between India and Sri Lanka—Silas (1967) reported that the most important prey items, in terms of biomass, of 40 longtail tuna (39.5–77.5 cm) were squids (Ommastrephidae), followed by crustaceans (stomatopods, mysids and megalopa) and a range of pelagic and demersal fishes representing families such as Engraulidae, Clupeidae, Syngnathidae, and Lutjanidae.

In contrast, two recent studies conducted in the coastal waters of the Arabian Sea off western India (Abdussamad et al. 2012, Mohammed Koya et al. 2018) found that longtail tuna primarily consumed teleosts (*Sardinella* sp., *Thryssa* sp., *Decapturus* sp., *Selar* sp., exoceotids, hemiramphids, *Megalaspis cordyla*, and *Auxis* spp.), followed by crustaceans (penaeids, portunids, and stomatopods), and cephalopods.

In the Sea of Japan, Kobayashi (2005) examined 242 fish (41–60 cm), of which 147 stomachs contained prey, and found them to primarily consume small schooling pelagic fishes (*Trachurus japonicus*, *Engraulis japonica*, and *Etrumeus teres*), and to a lesser extent cephalopods.

In the Gulf of Papua, Wilson (1981a) found 26 fish (< 70 cm) to primarily feed on small pelagic fish from the families Engraulidae and Scombridae, crustaceans (Alima, Decapoda and Penaeidae) and cephalopods.

One of the most comprehensive examinations of the feeding ecology of longtail tuna was a 2-year study of 497 fish sampled from northern and eastern Australia (Griffiths et al. 2007a). They recorded 101 prey taxa, with most the common taxa (in terms of biomass) being: small pelagic fishes (Engraulidae, Clupeidae, Scombridae, Belonidae and Hemiramphidae), demersal fishes (Carangidae, Leiognathidae and Sillaginidae), cephalopods (Teuthoidea and *Sepia* spp.) and crustaceans (Portunidae, Penaeidae and Squillidae). The study showed a distinct ontogenetic shift in feeding behaviour and diet after fish attained about 100 cm.

The diets of longtail tuna frequently contain demersal and benthic prey, most likely facilitated by their occupation of shallow coastal waters, that provides an important trophic linkage between pelagic and demersal components of the ecosystem, which differs from the role that larger tuna play in the trophodynamics of open ocean systems. For example, longtail tuna consumed fishes representing the families Leiognathidae, Mullidae, Gerridae, Gobiidae, Nemipteridae and Callionymidae in the waters of Australia and Papua New Guinea (Serventy 1942a, 1956; Wilson 1981a; Griffiths et al. 2007a), while 76% of the diet biomass of 112 fish (32–61 cm) examined from Malaysian waters in the South China Sea comprised *Monacanthus* spp. (Bachok et al. 2004). Off the coast of India, longtail tuna also consumed benthic species including *Platycephalus* spp. (Mohammed Koya et al. 2018), while in the Sea of Japan they often consumed the demersal *Apogon semilineatus* (Kobayashi 2005).

Interestingly, plastic materials have been documented in the diets of longtail tuna sampled from the waters around Australia, Indonesia, and India. Griffiths et al. (2007a) found three plastic drinking straws in the stomachs of longtail tuna in Moreton Bay, Australia—located adjacent to one of Australia's largest cities. Wagiyo and Febrianti (2015) and Mohammed Koya et al. (2018) did not report the type of plastic materials ingested by longtail tuna in Indonesian and Indian waters, but in terms of frequency of occurrence they comprised 1% and 8% of the diet, respectively. However, Mohammed Koya et al. (2018) described floating plastic debris aggregating small fish species that were commonly found in the stomachs of longtail tuna, and therefore ingestion of plastics is probably accidental whilst pursuing prey. Nonetheless, with the increasing incidences of plastics in the marine environment (Cózar et al. 2014), primarily from land-based sources, neritic predatory species such as longtail tuna, may be increasingly vulnerable to ingesting these plastics as they are transported by rivers and estuaries into coastal habitats, and further offshore where they have been found to be ingested by oceanic tunas such as yellowfin tuna (*T. albacares*) (Chagnon et al. 2018) and southern bluefin tuna (*T. maccoyii*) (Young et al. 1997).

Foraging behaviour and ecological role as prey

From two major longtail tuna research programs undertaken in Thailand (Yesaki 1982) and Australian waters (Griffiths et al. 2007a), a number of observations were made to describe the species' feeding behaviour and their predation by larger predators. For example, juvenile and small adult fish (< 70 cm) tended to form large schools and occupied an intermediate trophic level by primarily consuming small schooling baitfishes such as *Sardinella* spp., *Stolephorous* spp. and *Thyrssa* spp., and a wide variety of epipelagic crustaceans such as penaeids and *Portunus* spp. Fish of this size often form ripples on the surface when feeding, but they rarely leap from the water (Yesaki 1987). At these sizes, longtail tuna were often associated with other small neritic tunas such as kawakawa and frigate and bullet tunas. Together, these neritic tunas are important prey for larger predators. Although there are apparently no documented scientific identifications of longtail tuna in the diet studies of other predators, there are numerous anecdotal accounts from scientists and fishers who have witnessed the predation of longtail tuna. For example, small (< 60 cm) longtail tuna were observed in northern Australia to be predated upon by Spanish mackerel (*Scomberomorus commerson*), billfish (*Istiompax indica* and *Istiophorus platypterus*) and various carcharhinid sharks.

Larger longtail tuna (> 100 cm) are less commonly observed as surface aggregations and appear to feed in smaller schools (15–20 fish), and often as solitary individuals, attacking their prey in arrow formation with fish being equidistant to each other. In these cases, some fish have been observed leaping from the water. Fish of this size are near-apex predators in coastal ecosystems, such as Australia's Gulf of Carpentaria where they have an estimated trophic level of 4.62 (Okey et al. 2007). By comparison, oceanic tunas that support commercial tuna fisheries in a similar region of the western Pacific Ocean occupy higher trophic levels, such as bigeye (4.93) and yellowfin (4.78) tunas (Griffiths et al. 2019a).

Prey consumption rates

Longtail tuna are visual predators and primarily feed during the day, but feeding has been documented to occur during the night, but to a far lesser extent

(Griffiths et al. 2007a). Feeding intensity has also been shown in both Australian (Griffiths et al. 2007a) and Indian (Mohammed Koya et al. 2018) waters to have an inverse relationship with reproductive activity, indicating a possible energy investment for gonad development.

Prey consumption rates and daily ration of longtail tuna have been estimated by one study in Australian waters (Griffiths et al. 2007a), based on stomach content biomass and estimated prey evacuation rates. The study found that daily ration averaged 2.36% body weight (BW) day^{-1} but decreased with increasing fish size from 2.26% to 1.3% BW day^{-1} for fish < 100 cm and > 100 cm, respectively. In a concurrent study, Griffiths et al. (2007b) used commercial gillnet catch data to estimate a biomass of 12.07 kg km^{-2} for longtail tuna in the Gulf of Carpentaria (397,700 km^2). Using the longtail tuna biomass estimates coupled with the daily ration estimates, Griffiths et al. (2007a) estimated that 148,178 t $year^{-1}$ of prey were consumed annually in the Gulf of Carpentaria. Together, these studies demonstrated the important ecological role that longtail tuna play in Australian neritic ecosystems and are likely to play a similarly important role in other neritic ecosystems throughout their global distribution.

Habitat specificity and movement

Longtail tuna have been documented occupying water temperatures of 17–30 °C (Griffiths 2011, Mohri and Yoritake 2014). The optimal water temperature range for fish < 50 cm has been suggested to be 24–25.6 °C based on modelling of commercial catch data in relation to remotely-sensed sea surface temperature (SST) data in the Sea of Japan (Mohri et al. 2005, 2008). In Australia, Griffiths (2012) showed a seasonal spatial shift in recreational fishing effort for large longtail tuna (> 80 cm), which coincided with the southward movement of the EAC when SSTs were 18–22 °C, indicating that large longtail tuna probably prefer this range of SSTs.

In the first study of the habitat utilisation and movement of longtail tuna using electronic tags, Griffiths (2011) tagged nine longtail tuna (86–122 cm) with miniature pop-up archival tags ("miniPAT", Wildlife Computers) along the northern half of Australia's east coast. From the 494 days of data collected by the tags, fish dived to a maximum depth of 90 m and occupied water temperatures of 17.1–28.9 °C. However, tagged fish primarily occupied depths of less than 30 m and water temperatures of 20–28.5 °C (Fig. 3). Geolocation of tagged fish—estimated from the tag's archived light data—revealed fish did not move beyond the continental shelf, confirming the species' presumed preference for neritic waters. The data highlights the marked difference in movement and behaviour compared to other *Thunnus* species, particularly the absence of diving at dawn to remain at depth during the day and moving to surface waters during the night (Schaefer and Fuller 2002; Schaefer et al. 2007, Patterson et al. 2008). The restricted vertical movements of longtail tuna may explain its lack of a swim bladder as a possible adaptation for living in shallow neritic waters.

Very little information is available on the horizontal movements of longtail tuna. The historical low commercial value of longtail tuna in comparison to other commercially important tunas is likely the primary reason for the lack of a dedicated long-term tagging programs, and as a result, little is known of their movements throughout their distribution, with the exception of a few of opportunistic tagging studies. Raja Bidin (2002) tagged 8842 longtail tuna (15–47 cm) in Malaysian waters in the South China Sea over a period of 8 years. Unfortunately, only 19 tagged fish (23–46 cm) were recaptured, all of which were recaptured less than a year later within 180 nm of the release locations. In adjacent Indonesian waters, Kaltongga (1998) tagged 75 small longtail tuna (52–58 cm), but no recaptures were reported.

Wilson (1981a) recaptured 25 of the 414 fish tagged in the Gulf of Papua over a 2-year period. Although no information was reported on distances moved, all recaptures were made within the Gulf ($\sim$ 350 km wide) after being at liberty for 76–103 days.

Australia's NSW GTP has recapture information for 57 of the 3838 longtail tuna tagged by recreational fishers since 1974 (NSW DPI 2007). The movement data reveals that the species can move large distances in short periods. For example, the fish moving the

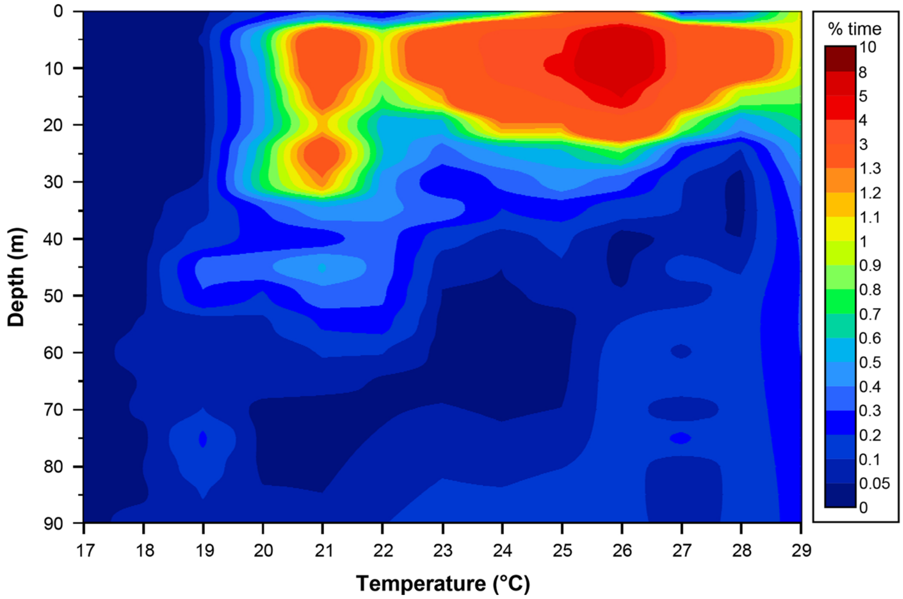

Fig. 3 Percentage of time that nine longtail tuna (86–122 cm) tagged with pop-up archival satellite tags off eastern Australia spent at temperature (°C) and depth (m). Data summarised from Griffiths (2011)

longest recorded distance was tagged in Moreton Bay, Queensland and was recaptured ~ 600 km to the south 24 days later (Fig. 4). The tagging data reveals that there may be a seasonal movement of fish as most fish tagged in Queensland waters that moved south into NSW waters were recaptured between March and May when the EAC is at its maximum southern extent (Ridgway and Godfrey 1997). Interestingly, the data also reveals that movement of fish tagged at some locations can be very limited, particularly within large marine embayments such as Moreton Bay and Hervey Bay. For example, of the 36 fish recaptured after being tagged in Moreton Bay, only four fish were recaptured outside of the bay, despite being at liberty for up to 3833 days. This may either reflect permanent residency within the bay or that the region is an annual visiting site during their presumed southward movement during summer and autumn (see Serventy 1956).

In contrast, all nine fish tagged with miniPAT electronic tags by Griffiths (2011) moved north for linear distances of up to 650 km. Two tagged fish - moved 450 km and 650 km north to a common area inside the Great Barrier Reef at times where spawning has been previously presumed to take place in October–March (Serventy 1956; Griffiths et al. 2019b). The remaining fish moved much shorter distances, with two fish occupying Hervey Bay for the entire 3-month duration of the tag deployments.

Fisheries

Longtail tuna is an important resource that is exploited in the waters of mainly developing countries bordering the western Pacific Ocean across to the northern Indian Ocean. As a result of their coastal distribution, longtail tuna are caught by small-scale commercial and artisanal fisheries in at least 21 countries throughout these regions (FAO 2019) primarily using purse-seine, gillnet, and hook and line (e.g. trolling), but also a variety of other minor methods including beach seine, stake traps, and set nets (Boonragsa 1987). Longtail tuna are caught in two broad fishery types differentiated by geography, the WCPO and the Indian Ocean, where the predominant gear used differs. Although longtail tuna comprise the majority of catches in the coastal tuna fisheries of both regions, they are not often targeted specifically. In the WCPO, longtail tuna constitutes a major component of the catches from multi-species fisheries for small neritic tunas and seerfishes, which primarily include kawakawa, frigate and bullet tunas, and Spanish (or King) mackerels

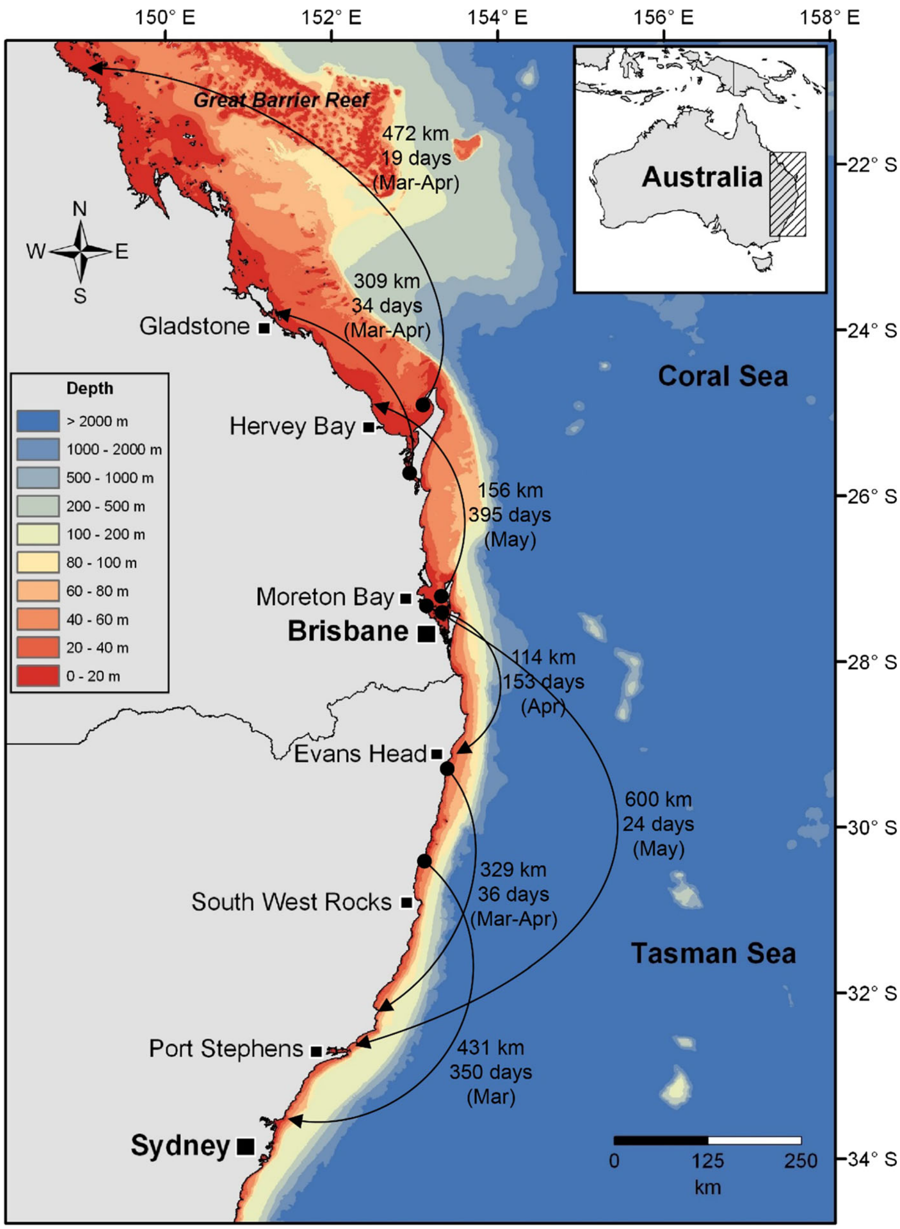

Fig. 4 Release and recapture locations of seven tagged longtail tuna that showed the largest movements among 55 recaptured fish from the New South Wales (NSW) Department of Primary Industries' Gamefish Tagging Program in Australian waters. Month of recapture and number of days at liberty is shown adjacent to each movement path

(*Scomberomorous* spp.) (Yesaki 1994). In the Indian Ocean, longtail tuna are generally larger and are caught in other multi-species drift gillnet fisheries that target larger oceanic tunas (e.g. yellowfin tuna) and sharks—particularly in Iran, Pakistan and India (MRAG 2012; Gerami and Dastbaz 2013).

WCPO fisheries

The major fisheries for longtail tuna in the WCPO operate in Southeast Asia, primarily the Gulf of Thailand and the South China Sea where small fish (15–55 cm) are primarily caught by purse-seine and drift gillnet, and to a lesser extent by hook and line (primarily trolling, but also includes handline and small longlines), particularly in Malaysia, Thailand, Vietnam, and Indonesia (Raja Bidin and Rumpet 1990; Kamarruddin and Raja Bidin 1991; Chullasorn 1995; Yonemori et al. 1995, Lewis 2006; Nootmorn 2015; Siriraksophon 2017).

The purse-seine vessels and gear used in this region range in their sizes depending on the types of sets intended to be made, such as those on fish aggregating devices (FADs) or free-swimming tuna schools during the day, or in association with luring light devices (e.g. electric lamps) during the night (Yonemori et al. 1995).

In general, vessels range from 18–24 m length overall (LOA) are crewed by 25–45 people and make short trips of around 1–4 days in duration (Boonragsa 1987; Merta 1987; Yonemori et al. 1995). The vessels are generally equipped with radar, echo sounders, and satellite navigational instruments (Chullasorn 1995). These vessels deploy nets having a stretched mesh size of 25–97 mm and range in length and depth of 500–1600 m and 50–150 m, respectively (Chullasorn 1995; Chantawong 1999). The smaller mesh sizes are primarily used for targeting small pelagic fishes (e.g. Indian mackerel, *Rastrelliger kanagurta*), whereas the larger mesh sizes are used to target tunas, including longtail tuna. In recent years, many purse-seine vessels have installed power blocks to reduce labour and to enable the use of longer and deeper nets (Chullasorn 1995).

In Thailand, small size classes of longtail tuna are caught in purse seine operations that target small pelagics, but they comprise a very minor component (0.39–1.9%) of the catch (Khemakorn and Vibunpant 2008). The main catches are in tuna nets using larger mesh sizes that take larger fish (Nootmorn and Tossapornpitakkul 2013). Interestingly, longtail tuna do not associate with FADs in the way that oceanic tuna species such as skipjack and yellowfin tuna do. Consequently, longtail tuna is not a target species as this fishery sets on FADs targeting small pelagics. Instead, longtail tuna are targeted in the early mornings when they generally school near the surface where they can be detected by sonar.

The second method that accounts for a large proportion of the longtail tuna catch in the WCPO is drift gillnet, often known as Spanish (or King) mackerel drift gillnets, since the primary target species are *Scomberomorus* spp. (Chullasorn 1995). Drift gillnet vessels are often 14–18 m LOA and operated by up to 10 crew members, who undertake trips of 1–4 days in duration (Yonemori et al. 1995). Gillnets usually consist of 60–120 mm stretched monofilament mesh of 1–12 km in length and around 7–50 m in depth, depending on the location (Boonragsa 1987; Chullasorn 1995; Yonemori et al. 1995).

The hook and line (i.e. trolling) vessels are much smaller in size (7–18 m LOA)—often fitted with outboard engines (16–55 hp)—and make trips of 1–15 days in duration (Yonemori et al. 1995, Tampubolon et al. 2015). Given the small size of the vessels, fish are kept on ice until returning to port. Each boat has a crew of 1–5 fishers who generally deploy up to 12 trolling lines, some with branchlines, fitted with various types of lures or baits (Merta 1987). Some trolling techniques such as the "Rintak" (translating to "thousand lines") used in southern Indonesia, appear more like a longline, with 100–120 branchlines fitted with lures that are attached to a mainline (Tampubolon et al. 2015).

It is also noteworthy that longtail tuna are caught in reasonable quantities in unique multi-species set net fisheries in coastal waters of Japan (Nakamura 1969; Mohri et al. 2010, 2013) and Taiwan (Chiang et al. 2011), where complex net arrangements set adjacent to a major current corral migrating fish into a central net pocket (Chiou and Lee 2004).

The composition of the WCPO longtail tuna catch by gear type has changed considerably over the history of the fishery. When disaggregating the catch into three separate time periods, each of 15 years (1972–1986, 1987–2001, 2002–2016), purse-seine attributed 60.6%, 81.3% and 88.0% to the WCPO catch, respectively, while the contributions by gillnet and hook and line decreased considerably (Fig. 6).

Indian Ocean fisheries

In contrast to the WCPO fisheries that catch longtail tuna, the fisheries in the Indian Ocean generally catch larger fish (60–80 cm) primarily using drift gillnets and to a lesser extent purse-seine—especially in the waters of Thailand and Malaysia—and hook and line (trolling). These catches are usually made in coastal regions of the northwestern Indian Ocean from the west coast of India to Somalia, particularly in countries bordering the Gulf of Oman, Persian Gulf, Red Sea and the Gulf of Aden (Prabhakar and Dudley 1989; Kahraman et al. 2011). Off the west coast of

Malaysia, longtail tuna is primarily a bycatch in the small pelagics fishery that uses lights and/or FADs, as is the case in Thailand. Between 2006 and 2011, neritic tunas accounted for 9% of the catch in the Strait of Malacca, with longtail tuna accounting for just over half of the landings (Basir and Jamon 2012). Over the history of the neritic pelagic fishery in the Indian Ocean, the methods used that account for the majority of the longtail tuna catch has remained very consistent, with drift gillnet being responsible for 18.8%, 19.0% and 18.2% of catches for three time periods (1972–1986, 1987–2001, 2002–2016), respectively.

Much of the drift gillnet catch of longtail tuna is contributed by Iran, Pakistan and India, from vessels of 10–30 m LOA and 1–1.5 t capacity that are generally equipped with iced fish holds, hydraulic net haulers, GPS, and echo sounders (Moazzam and Nawaz 2014). The gillnets are made of polyamide or polyethylene monofilament material of 90–170 mm stretched mesh with a length and depth of 4.83–11.27 km and 14 m, respectively (Pillai et al. 2003, Gerami and Dastbaz 2013; Moazzam and Nawaz 2014). The nets are generally set in the evening and retrieved during the early morning.

The drift gillnet fishery has a long contentious history with conservation groups since the relatively unselective gear has very high catch rates of a variety of bycatch species, including turtles, cetaceans, and elasmobranchs. In a recent study of the bycatch of Pakistan's tuna drift gillnet fishery, it was estimated that 28,000 sea turtles and 12,200 cetaceans were caught annually between 2011 and 2013 (Moazzam and Nawaz 2014). However, in order to reduce the entanglement and mortality of cetaceans and sea turtles, WWF-Pakistan promoted the introduction of subsurface gillnetting in 2015—wherein the gillnets are set 2 m below the surface—that is now adopted by the entire gillnet fleet of Pakistan. This has resulted in major decrease in entanglement of sea turtles to around 2,700 per year in 2015–2016, while for cetaceans, entanglement decreased to 480 and 280 individuals in 2016 and 2018, respectively (Moazzam and Nawaz 2017; Kiszka et al. 2018). By comparison, Iran's drift gillnet fisheries were estimated by Anderson (2014) to catch between 24,694 and 101,345 cetaceans per year—based on the catch rates reported by Yousuf et al. (2009) and Leatherwood (1994), respectively.

In contrast to the WCPO, purse-seine has accounted for comparatively little (18–19%) of the longtail tuna catch over the history of the neritic tuna fishery, while hook and line (primarily trolling) has also accounted for a minor component (9–12%) of catches (Fig. 6).

There appears to be little country-specific published information on the configuration of vessels and the gear used for the purse-seine and hook and line fisheries in the neritic tuna fisheries in the western Indian Ocean. However, there is some basic information available on Iran's and Oman's purse-seine and troll fisheries that operate in the Gulf of Oman and the Persian Gulf that account for a significant component of the longtail tuna catch in the western Indian Ocean. Thai purse-seining is carried out in the same manner as for the South China Sea, from purse-seine vessels ranging in length from 55–99 m LOA (Moradi 2015) and equipped with modern electronics including GPS and echo sounders (Parsa et al. 2018). The vessels are crewed by 30–35 people undertake voyages of 2–4 weeks in duration (RECOFI 2013b). The typical configuration of the purse-seine net is similar to gear used in the WCPO in terms of length (1886 m) and depth (210 m), but the net has a much smaller stretched mesh size of 16–20 mm (Hosseini and Ehsani 2014; Parsa et al. 2018).

The hook and line fishery for neritic tunas in the northwestern Indian Ocean almost exclusively involves trolling from outboard-powered vessels of less than 15 m LOA, where 3–4 crew operate single day trips in coastal waters and fish kept in ice until returning to port (RECOFI 2013c; Kakoolaki 2017). Some of the larger vessels venture further offshore, equipped with freezers or ice holds to facilitate trips of 1–2 weeks in duration (RECOFI 2013a). The specific configuration of the troll gear is not well documented, however, it is likely to be similar to trolling methods used to target neritic tunas in Southeast Asia, which consist of several lines and hooks. Yesaki (1994) suggested that one line with a single hook, most likely a lure, is fished from the stern of the smaller vessels in the north Arabian Sea.

Commercial catches

India, Indonesia, Madagascar and the United Arab Emirates were the first countries in FAO records to report catches of longtail tuna, with the total reported catch being 796 t in 1950 and increasing to 2,038 t by

1960. By 1987, 11 countries reported landings of longtail tuna, taking a combined annual catch of 90,122 t (Fig. 5a). The year 1988 marked the beginning of a significant change in the catch trend that indicated a possible focus on targeting longtail tuna, with the annual reported catch almost doubling to 168,330 t in just 1 year. This was primarily due to significant increases in the reported catches by the large-scale purse-seine fisheries in both Taiwan (7,080 t to 26,120 t) and Thailand (39,180 t to 92,925 t) in the WCPO, which persisted until 1992 (Fig. 5c). These catch increases roughly coincided with steady increases in annual catches in the Indian Ocean, particularly by Iran and Oman, that averaged around 46,000 t (Fig. 5b).

The total global catch continued to increase through the late 1990s but rapidly began to accelerate from 2002 to in excess of 208,000 t per year and reaching a peak 291,264 t in 2007 (Fig. 5a). Again, this was due to a combination of increased catches in both the WCPO and Indian Ocean. In the WCPO, this was mainly due to the commencement of catch reporting by Indonesia catching 70,735 t in 2004 and annually averaging 72,005 t (± SD 24,719) thereafter until 2017 (Fig. 5c), which was primarily caught by purse-seine (Fig. 6). However, it is important to note that Indonesia's sudden catch increase may be a possible artefact of misidentification and misreporting. In Malaysia and Indonesia, longtail tuna is locally known as "Tongkol abu abu", while small-sized tunas—including neritic species such as longtail tuna, kawakawa, frigate and bullet tunas, as well as juvenile oceanic tunas including yellowfin, bigeye and skipjack tunas—are collectively referred to as "Tongkol" (Ingles et al. 2008).

In the Indian Ocean, the dramatic increase in catches from the early 2000s was primarily due to increasing drift gillnet catches by Iran and a number of coastal States in the western Indian Ocean, but also India, Malaysia and Thailand fishing in the Andaman Sea (Fig. 5). The increase in catches by Iran and Pakistan has been attributed to the increase in Somali piracy that intensified from around 2008 in the western Indian Ocean, primarily in Somali waters and adjacent Areas Beyond National Jurisdiction (ABNJ). This forced a significant proportion of the effort by large-scale industrial tuna fleets that would normally fish beyond their national EEZs in the northwestern Indian Ocean to retreat to more coastal waters to target longtail tuna in their EEZs since at least 2009 (Akhondi 2012; Al-Kiyumi et al. 2014, Moazzam 2014), since Iranian and Pakistani vessels have dual registration in both countries (Moazzam 2012b). In Iran alone, this resulted in an increase in longtail tuna catch from 25,000 to 81,000 t between 2006 and 2011 (Akhondi 2012). Over the past 5 years, Indonesia, Iran, Malaysia, Thailand, Oman, Pakistan and India have collectively contributed 98% to the global reported catch (Fig. 5a).

In Oceania there is no significant commercial fishery for longtail tuna, despite their abundance and large size. Although FAO statistics reveal no commercial longtail tuna catches being reported for Papua New Guinea—the easternmost extent of the distribution of longtail tuna—Wilson (1981a) reported a small commercial fishery consisting of up to 26 vessels existed in the Gulf of Papua in the mid-1970s that generally caught less than 100 t per year. He also described a small and seasonal (November to April) artisanal and subsistence fishery that operates in the Gulf of Papua that was estimated to take less than about 10 t of longtail tuna annually. No commercial or artisanal catches have been reported for other nearby Pacific Island Nations, such as the Solomon Islands, Vanuatu, Fiji, New Caledonia, or New Zealand.

In Australia, longtail tuna were fished since at least 1897 (Serventy 1956), but catches between 1950–2014 have averaged about 34 t and peaking at just 138 t in 1985 (FAO 2019). These low catches in Australia generally reflected a historic low domestic market demand for tuna. Catches by Australian flagged Taiwanese gillnet vessels—managed by the Australian Fisheries Management Authority (AFMA) under a temporary bilateral agreement in the Australian Fishing Zone (AFZ)—off northern Australia between 1974–1986 ranged between 200–2000 t per year whilst primarily targeting sharks and narrow-barred Spanish mackerel (*Scomberomorus commerson*) (Stevens and Davenport 1991). Although there has been various proposals over the past few decades to develop a commercial neritic tuna fishery in northern Australian waters (Robins 1975; Wilson 1981b; Lyle and Read 1985), the high incidental mortality of cetaceans caught by the Taiwanese gillnet operations in the AFZ—estimated to be ~ 14,000 animals in 1981–1985 (Harwood and Anderson 1987)—has since halted any subsequent

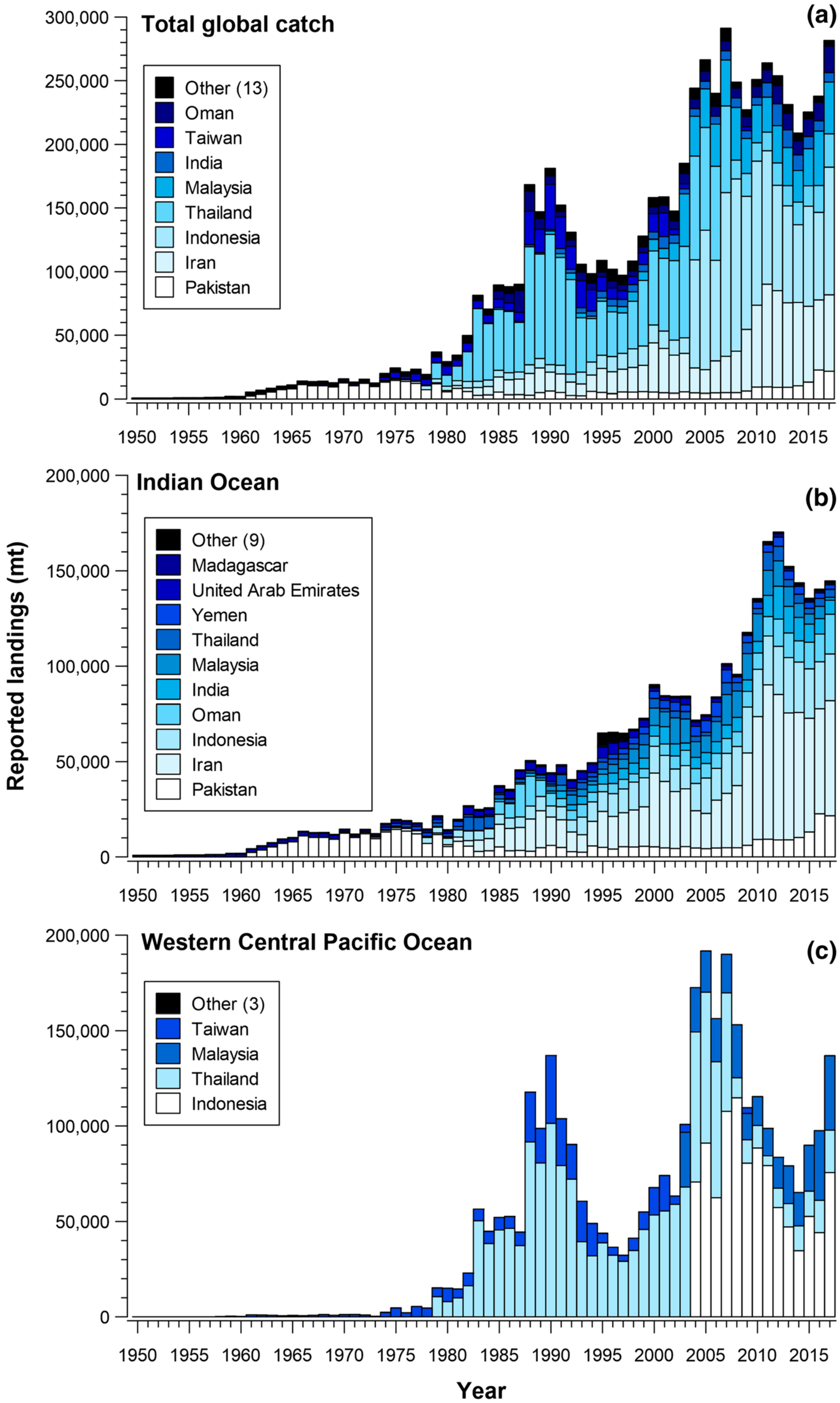

Fig. 5 Annual reported catches of longtail tuna by country having the highest catches for the years 1950–2017 **a)** globally, **b)** in the Indian Ocean, and **c)** in the western and central Pacific Ocean (Data source: FAO 2019). Catches for all other countries are combined in the "other" category

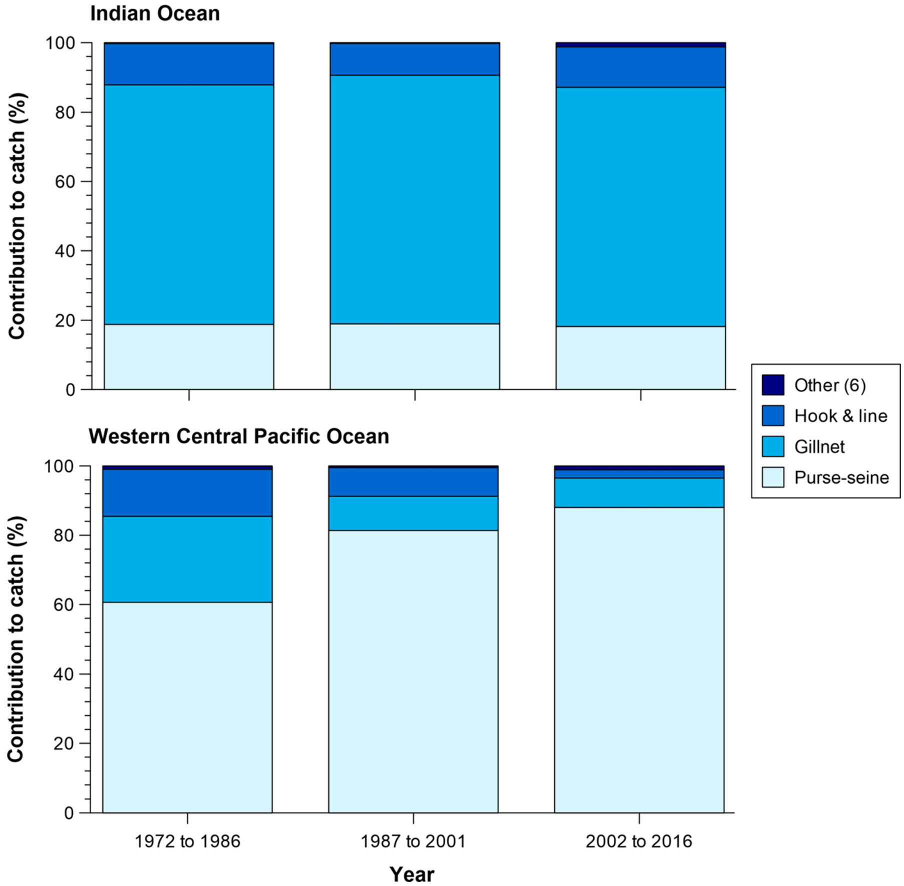

Fig. 6 Percentage of total catches by gear type during three time periods (1976–1986, 1987–2001, 2002–2016) for the Indian Ocean (Data source: IOTC 2018) and the Western Central Pacific Ocean (Data source: SEAFDEC 2018). Number of gear types included in the "other" category shown in parentheses

considerations for the development of a similar domestic drift gillnet fishery.

It is important to note that the landings data presented in this paper, sourced from RFMOs, RFBs or national fisheries agencies, are likely to suffer from a number of significant shortcomings. Firstly, because longtail tuna comprise important artisanal and subsistence fisheries in many developing countries, where vessel logbook reporting is either not in place or strictly enforced, reported landings from these countries are likely to be underestimated. This issue is significant for countries such as Somalia, where no compulsory reporting of catches is required and validation of catches by domestic or international fisheries agencies is difficult and dangerous (IOTC 2015; Persson et al. 2015). In a recent reconstruction of Somali catches, Persson et al. (2015) estimated that the catch by the artisanal fleet alone (32,730 t) exceeded the official landings reported to the FAO for all fisheries combined (29,800 t) in 2010. They estimated that 5% of the artisanal catch was composed of longtail tuna ($\sim$ 1,600 t), which is not currently included in FAO catch statistics. Similar catch reconstructions for Pakistan's commercial tuna drift gillnet fishery revealed that the reported catch of longtail tuna in 2015 ($\sim$ 7000 t) was 58% lower than the reconstructed catch ($\sim$ 15,000 t) (Moazzam and Ayub 2017).

Catches may also be underestimated in some countries due to non-reporting or under-reporting for various political reasons. For example, Taiwan historically reported annual catches of several thousand tonnes to SEAFDEC and the FAO since at least 1986, but annual catches abruptly dropped to zero after 2003, with the exception of 2980 t being reported in 2009 (Fig. 5c), suggesting Taiwan may no longer completely report their catches. In a reconstruction of Tawian's fishery catches from 1950–2007, Kuo and Booth (2011) estimated that around 400,000 t of catch was unreported since 2003. The majority of this unreported catch was believed to be from coastal fisheries, including the set-net, gillnet, and small purse-seine fisheries that are responsible for the majority of the catch of neritic tunas in Taiwan (Chiou and Lee 2004).

Similarly in Australia, despite the Australian-flagged Taiwanese gillnet fleet reporting annual landings of up to 2000 t between 1976 and 1984 (Stevens and Davenport 1991), the catch statistics for this period are still not appear to be accurately reflected in FAO statistics. More recently, longtail tuna are still captured in large numbers in northern Australia's State-managed offshore and inshore shark and mackerel (*Scomberomorous* spp.) gillnet fisheries, however they are generally an unreported discarded bycatch.

Misidentification and mis-reporting of longtail tuna has been a fundamental problem in some countries, especially throughout Southeast Asia. It has only been recently determined that catches of "Tongkol"—a species complex of small sized tunas—in Indonesia, in particular West Sumatra, has primarily been attributed to longtail tuna and has therefore probably resulted in significant overestimates of the catch (Geehan 2016). Similar reporting issues appear to be evident in Japan where generic names such as "Shibi" (Itoh et al. 1996) and "Yokowa" are used for reporting species complexes of small-sized tunas, which include longtail tuna (Itoh et al. 1996, Mohri et al. 2008). This likely explains the dramatic increase in longtail tuna catches in the WCPO region from 2004 and the subsequent rapid decline since around 2011 (Fig. 5c) following improvements in port sampler training and reporting protocols (Geehan 2016). Although longtail tuna is a commonly caught species throughout parts of Indonesia, there is now great uncertainty over the extent of over-reporting of longtail tuna in previous years, and whether further improvements in observer training can overcome these fundamental issues that severely compromise the data available for future assessments, for not only longtail tuna, but the several other principal commercial tuna species that have been incorporated into the "Tongkol" taxonomic aggregation.

Similarly in Japanese waters, small longtail tuna (< 50 cm FL) occur sympatrically with small Pacific bluefin tuna (*T. orientalis*) and/or yellowfin tuna (*T. albacares*) and the species complex is commonly reported in different regions as "Shibi" (Itoh et al. 1996) or "Yokowa" (i.e. "juvenile tuna") (Mohri et al. 2008). Interestingly, no catches of longtail tuna appear in official FAO statistics for Japan, despite the fact they are frequently caught throughout the East China Sea and the Sea of Japan in quantities in the order of at least hundreds of tonnes in the set net fishery alone (Itoh et al. 1996, Kawatsu et al. 2011). It is possible that similar reporting and species identification issues are evident in other coastal States where a mixture of neritic and oceanic tunas are caught, or at least brought together at central landing sites.

Recreational fisheries

Longtail tuna are important to recreational (sport) fisheries in a small number of countries throughout their range, particularly in Australia, Oman, Kenya, Mozambique, Pakistan, Thailand, Malaysia and Indonesia (Wekesa and Ndegwa 2011; Griffiths et al. 2013, Chacate and Mutombene 2014; Hornby et al. 2014). In countries such as Australia and Oman, they are highly regarded for their large size and fighting ability, and because they can generally be targeted from small vessels in relatively sheltered inshore waters. In contrast, in other countries in Southeast Asia, longtail tuna are generally much smaller (< 50 cm FL) and are used as bait (alive or dead) to target large billfishes (Istiophoridae spp.), tunas and sharks.

In Australia in particular, longtail tuna has grown in popularity in recent years, with several annual catch and release tournaments being established to solely target the species, particularly by saltwater fly anglers. This is probably helped by the presence of large longtail tuna in Australia waters, with all 33 International Game Fish Association (IGFA) world line class records for the species—including the all-tackle world record of 35.9 kg—primarily coming from Australia's east coast (IGFA 2017).

In recognition of the importance of longtail tuna to recreational fisheries in Australia, the species was declared a 'recreational-only' species by the Commonwealth government in December 2006, with an annual bycatch quota of 70 t allocated to multi-species Commonwealth commercial fisheries and a 10-fish trip limit to allow for incidental catches in fisheries that may have difficulty in eliminating longtail tuna captures due to the regions fished and the selectivity of the fishing gears (e.g., gillnet fisheries targeting sharks and *Scomberomorus* spp.) (Borthwick 2012). The recreational catch of longtail tuna is managed by individual State government fisheries agencies. Each State imposes slightly different regulations, but generally longtail tuna are managed through minimum size limits and daily catch limits. For example, in New South Wales, there is a per person possession limit of 2 and 5 fish for longtail tuna above 90 cm TL and less than 90 cm TL, respectively.

Very few data sources exist to accurately determine the magnitude of catches of longtail tuna by recreational fisheries, mainly due to the species being targeted by specialised fishers who are infrequently intercepted in recreational fishing surveys that are usually designed to sample generalist fishers (Griffiths et al. 2013). The specialised land-based gamefish fishery along eastern Australia was surveyed by Griffiths (2012) to estimate catch rates for species such as longtail tuna. Catch rates were found to be very low, with fishers catching one longtail tuna for every 62.5 h of effort expended (0.016 fish hr^{-1}). This was due to a high average trip effort (9.44 ± SD 6.65 h), which contributed AU$1735 (± 788) per fisher annually to local economies.

In a subsequent Australian nation-wide survey of longtail tuna catches by boat-based and land-based recreational fishers, 8 t were reported to have been caught in 2009 by the 1182 sport fishers surveyed. Given there are an estimated 3.6 million recreational fishers in Australia, of which approximately 5% target tunas (Henry and Lyle 2003), it may be conceivable that the recreational catch may exceed 1000 t per year.

In Kenya and Mozambique, longtail tuna comprise a suite of near-shore tuna and tuna-like species that are targeted by recreational fishers in small boats (3–9 m) (Wekesa and Ndegwa 2011; Chacate and Mutombene 2014). The recreational fisheries in either country have not been the subject of detailed scientific surveys. In Kenya, Wekesa and Ndegwa (2011) used the voluntery catch records from a single sport fishing club in Kenya to estimate a recreational catch of 3.3 t for longtail tuna. Similarly, Chacate and Mutombene (2014) used voluntary submission of catch cards from the ~ 2700 licenced recreational fishers in Mozambique and estimated a total catch of 125 t. Given the high frequency of non-reporting by Mozambique fishers (Chacate and Mutombene 2014), and that the surveys did not sample all fishing clubs or fishers who are not members of clubs, these catch estimates are most likely underestimated.

Utilisation and marketing of longtail tuna

Despite being lesser known than some of the oceanic tunas, such as skipjack and yellowfin tuna, longtail tuna has established markets in canned and fresh forms both in domestic and export markets. Longtail tuna is most widely used in canned form, being processed in a small number of plants primarily in Iran, India, Indonesia, and Thailand, which also process other principal tuna species such as skipjack, albacore and yellowfin tuna. The canned product is then exported to countries including the United States, Australia, Finland and Sweden (Asia–Pacific Fishwatch 2019).

In Thailand, longtail tuna destined to be canned for export are delivered to the cannery directly from purse seine vessels unloading fresh fish at local ports, or they are imported frozen. Once at the cannery, the fish are graded for size and quality before being cooked. The meat is removed manually and placed in cans prior to vacuum sealing and labelling (Asia–Pacific Fishwatch 2019).

In Bitung, Indonesia, some longtail tuna is packed in catering-sized cans destined for the food service market in the USA. However, most is packed in consumer-sized cans under a variety of labels and sold to small retailers. Some of the larger tuna companies that focus on processing skipjack and yellowfin tunas also produce small volumes of longtail tuna as an alternative for consumers who prefer 'white meat' albacore tuna, particularly in some Middle Eastern countries, such as longtail tuna is a popular as a canned white meat tuna. In the United Arab Emirates about 30% of the canned market is for white meat (albacore and longtail tunas) (Asia–Pacific Fishwatch 2019).

In addition to canning and fresh fish, in some countries longtail tuna is smoked or used as sashimi. In Indonesia, longtail tuna is hot smoked—known as "Fufu/ikan asar"—in the same way in which skipjack is prepared. Longtail tuna is used for sashimi in Japan, and most likely other countries in Southeast Asia, although Japan's reasonably small catches of longtail tuna mean that it is generally not widely or consistently available to consumers (Zennic 2016).

In Pakistan, longtail tuna are generally not consumed locally but are salted and dried and exported to Sri Lanka (Moazzam 2012a). However, since 2003, all longtail tuna and other tropical tunas (yellowfin and skipjack) are transported either by land or carrier vessels to Iran (Moazzam 2012a). It is believed that the majority of the tuna product sent from Pakistan to Iran is reflected in the annual landings of Iran, which may explain the relatively smaller annual catches by Pakistan (see Fig. 5b).

Stock assessment

There have been at least seventeen stock assessments of longtail tuna conducted in various regions throughout their geographic distribution. Despite available genetic and length-frequency data from fishery catches providing some evidence of the possible existence of at least four main putative stocks—Oceania, Southeast Asia, western Indian Ocean, and eastern Indian Ocean (Fig. 2)—the majority of assessments did not define the spatial extent of the stock, but instead generally used political boundaries. Of the assessments that are hereafter summarised, ten used yield per-recruit (YPR) models—with length- or age-frequency data to derive biological and mortality parameters—one assessment applied a stock production model to standardized CPUE data for the drift gillnet fishery, while four assessments of the entire Indian Ocean used a range of data-poor assessment models based on annual catches for all fisheries combined (Table 3).

The assessments defined stock status using a range of biological reference points (BRPs), making direct comparisons between assessments difficult in many cases. Some of the more rigorous assessments used F_{MSY}, B_{MSY}, and SB_{MSY}, which define the instantaneous fishing mortality rate (F year^{-1}), annual stock biomass (B) and spawning stock biomass (SB) at maximum sustainable yield (MSY), respectively. Some assessments used the precautionary $F_{0.1}$ BRP, which is the F where the slope of the YPR curve is 10% of the slope of the curve at its origin. The YPR BRPs of F_{MAX} and E_{MAX} is the value of F and exploitation rate (E) where yield is maximised. Here, E is defined as $E = F/(F + M)$, where M is the instantaneous natural mortality rate.

None of the stock assessments defined whether the reported BRPs used were target or limit references points. To be precautionary in this paper, BRPs were assumed to be limit reference points. Therefore, values of ≥ 1 for F/F_{MSY} or $F/F_{0.1}$ indicate the stock is subject to overfishing (i.e. growth overfishing), whereas values of ≤ 1 for B/B_{MSY} or SB/SB_{MSY} indicate the stock is overfished (i.e. recruitment overfishing). For the more rudimentary assessments, that are often undertaken using ELEFAN or FiSAT software, E has been used as the BRP. In these assessments, values greater than 0.5 were assumed to indicate the stock was subject to overfishing, since $E = 0.5$ has been considered a proxy for MSY (Gulland 1985). The BRP $F_{x\%}$ is the value of F at which the spawning potential ratio (SPR) has been reduced to x% (usually in the range of 20–40%) of the spawning stock in the absence of fishing ($F = 0$) (Gabriel and Mace 1999).

Hereafter, we summarize the results of these stock assessments by ocean basin, although the validity of the outcomes need careful consideration as some of the data inputs are highly uncertain. For example, assessments that only produce a value for E from length-frequency analysis are likely to have higher uncertainly in determining stock status than statistical models that produce estimates of F, F_{MSY}, B_{MSY}, and SB_{MSY} from time series of catch and effort data.

Eastern Indian Ocean

There have been at least six stock assessments of longtail tuna in the eastern Indian Ocean all being conducted off the west coast of India in the Arabian Sea and apparently none being undertaken off the east coast in the Bay of Bengal (Table 3). All of these assessments used YPR models, and generally analysed length-frequency data to derive biological and mortality parameters, and so their results should be used with caution. In an assessment of the stock in western Indian waters using a YPR model for the period 1984–1988, James et al. (1992) estimated an E of 0.397 year^{-1} for commercial and artisanal fisheries and concluded the stock was approaching full exploitation. A subsequent YPR analysis for the period 1997–2002 (Pillai et al. 2011) indicated that E had steadily increased to 0.81 year^{-1} in 2002, which was in the vicinity of E_{MAX}. They noted a progressive decline in the mean size of fish in catches and

Table 3 Summary of stock assessments conducted on longtail tuna categorised by putative stock (see Fig. 2), including countries involved, study source, assessment year(s), model and data type used, fishing mortality (F year^{-1}), exploitation rate (E), biological reference point(s) (BRP) used and their values, and the status of the stock shown as: Overfishing not occurring (ON), Overfishing occurring (OO), Not overfished (NO), Overfished (OF). Assessment models were: Stock Reduction Approaches (SRA), Stochastic Stock Reduction Approaches (SSRA), Optimised Catch Only Method (OCOM), A Stock Production Model Incorporating Covariates (ASPIC), and yield per-recruit (YPR). Assessment parameters that were not reported, or unable to be calculated using other reported parameter values, are shown as "NR"

Stock	Country/region	References	Assessment period	Model type	Data type	F year^{-1}	E year^{-1}	BRPs	BRP values	Status
Pan-Indian Ocean	Ocean-wide	Zhou and Sharma (2014)	2012	SRA	Catch	NR	NR	F/F_{MSY}	1.08	OO
								B/B_{MSY}	1.12	NO
	Ocean-wide	Martin and Sharma (2015)	2013	OCOM	Catch	0.433	0.419	F/F_{MSY}	1.11	OO
								B/B_{MSY}	1.02	NO
	Ocean-wide	Martin and Robinson (2016)	2014	OCOM	Catch	0.402	0.401	F/F_{MSY}	1.03	OO
								B/B_{MSY}	0.99	OF
	Ocean-wide	Martin and Fu (2017)	2015	SSRA	Catch	0.818	0.577	F/F_{MSY}	3.27	OO
								SB/SB_{MSY}	1.02	NO
Western Indian Ocean	Oman	Prabhakar and Dudley (1989)	1987–1988	YPR	LF	1.355	0.760	E_{MAX}	0.73	OO
	Oman, Pakistan, Yemen, Iran	Al-Kiyumi et al. (2014)	2012	ASPIC	CPUE	1.3	NR	F/F_{MSY}	1.38	OO
								B/B_{MSY}	1.01	NO
	Iran	Yasemi et al. (2017)	2014	YPR	LF	0.720	0.630	E	0.50	OO
	Iran	Darvishi et al. (2018)	2015–2016	YPR	LF	1.090	0.690	F_{MAX}	0.85	OO
								$F_{0.1}$	0.47	OO
								$F_{20\%}$	0.17	OF
Eastern Indian Ocean	India	James et al. (1992)	1984–1988	YPR	LF	0.584	0.397	E_{MAX}	0.79	ON
	India	Ghosh et al. (2010)	2003–2006	YPR	LF	0.720	0.640	E_{MAX}	0.64	OO
	India	Pillai et al. (2011)	2001–2002	YPR	LF	3.414	0.810	E_{MAX}	1.00	OO
	India	Abdussamad et al. (2012)	2008–2010	YPR	LF	2.940	0.790	E_{MAX}	0.80	OO
								$F_{10\%}$	0.09	OF
	Andaman Sea, Malacca Strait	Nishida et al. (2016)	2014	ASPIC	CPUE	0.566	NR	F/F_{MSY}	1.11	OO
								B/B_{MSY}	0.89	OF
	Malacca Strait	Wagiyo and Febrianti (2015)	2014	YPR	LF	2.07	0.51	E	0.50	OO
Southeast Asia	Malaysia	Raja Bidin and Rumpet (1990)	1998–1992	YPR	LF	1.439	0.630	E_{MAX}	0.49	OO
	South China Sea	Nishida et al. (2016)	2014	ASPIC	CPUE	0.193	NR	F/F_{MSY}	0.18	ON
								B/B_{MSY}	2.22	NO
	Indonesia	Restiangsih and Hidayat (2018)	2014	YPR	LF	1.01	0.62	E	0.50	OO
Oceania	Australia	Griffiths (2010)	2002–2004	YPR	AF	0.209	0.369	F_{MAX}	0.59	ON
								$F_{0.1}$	0.33	ON
								$F_{40\%}$	0.39	NO

recommended caution be exercised in any further consideration of fishery expansion. A third assessment undertaken in the same region for the period 2003–2006 (Ghosh et al. 2010) estimated E to be 0.64 year^{-1}, which exceeded E_{MAX} by around 40%. Based on the assessment results, the authors recommended a reduction in fishing effort, or at least diversion of effort to deeper offshore waters, especially by large factory purse-seine vessels. The most recent assessment in Indian waters was conducted for the years 2008–2010 (Abdussamad et al. 2012) and indicated that E remained high (0.80 year^{-1}), exceeding the estimated E_{MAX} of 0.63 year^{-1}, which was substantially lower than previous assessments due to the inclusion of updated biological parameters. Their analysis indicated that the stock biomass had declined to just 9.4% of the unexploited biomass and recommended management action be taken to reduce the fishing mortality on small fish (< 50 cm FL).

Further to the east, Wagiyo and Febrianti (2015) undertook a stock assessment of longtail tuna in the Malacca Strait using a YPR model based on monthly length-frequency samples taken from the port of Langsa during 2014. They estimated a high F (2.07 year^{-1}) and E of 0.51 year^{-1}, which exceeded their E BRP of 0.50 year^{-1}, implying the stock is subject to overfishing.

Two stock assessments were initiated by SEAFDEC by Nishida et al. (2016) to characterise two putative stocks for 2014; the region of the Indian Ocean including the Andaman Sea and Malacca Strait and the Pacific region incorporating the South China Sea (see *Southeast Asia*). The Indian Ocean assessment is one of the most reliable assessments available for longtail tuna that utilised CPUE data in ASPIC models to conclude that the stock was subject to overfishing (F/F_{MSY} = 1.11) and overfished (B/B_{MSY} = 0.89). The authors recommended a reduction in catch and fishing effort by around 10%, despite the catch being around one third of the catch in the adjacent stock in the South China Sea.

Western Indian Ocean

There have been at least four stock assessments of longtail tuna in the western Indian Ocean, all using YPR models based on length-frequency data. Again, the reliability of the input data and subsequent stock status for the four assessments is highly uncertain and therefore the results need to be viewed with caution. An assessment in Omani waters—primarily in the Gulf of Oman—was undertaken by Prabhakar and Dudley (1989) produced an E of 0.760 year^{-1}, which was slightly less than the estimated E_{MAX} of 0.727 year^{-1}, leading to the conclusion that the stock was probably fully exploited and recommended no further increase in fishing effort.

In a similar region encompassing the Persian Gulf and the Gulf of Oman, Al-Kiyumi et al. (2014) used standardized CPUE data from the Omani drift gillnet fishery in A Stock Production Model Incorporating Covariates (ASPIC). The model indicated that the stock in 2012 was subject to overfishing (F/F_{MSY} = 1.38) and was in bordering on an overfished state (B/B_{MSY} = 1.01). In a subsequent assessment for 2014 using a YPR model, Yasemi et al. (2017) estimated F (0.720 year^{-1}) for the commercial drift gillnet fishery to be half that of Al-Kiyumi et al. (2014), but it still produced a high E (0.626 year^{-1}) that far exceeded their estimated E BRP of 0.50 year^{-1}. These results led the authors to conclude that "the population of longtail tuna in the waters of northern Persian Gulf and Oman Sea is being heavily exploited and overfished at a higher level than the optimum and a better management policy is necessary in this area".

In the most recent assessment, conducted in Irani waters including the Persian Gulf and the Oman Sea, Darvishi et al. (2018) determined that F had further increased to 1.090 year^{-1} since previous assessments in the region. They estimated the YPR BRPs of F_{MAX}, and $F_{0.1}$ to be 0.85 and 0.47, respectively, and that the population biomass was 17.2% of the unexploited biomass at the current F value. From these results the authors concluded the stock is subject to overfishing and is overfished (Table 3).

Pan-Indian Ocean

In 2014, the IOTC—in conjunction with their Working Party on Neritic Tunas established in 2012—began to solicit the development of data-poor methods for assessing the stock status of neritic tunas and seerfishes across the entire India Ocean. Although the input data and stock status in the assessments described herein contain significant uncertainty, this uncertainty is quantified statistically, and therefore these assessments are among the most reliable for the species to date.

Zhou and Sharma (2014) used traditional Stock Reduction Analysis (SRA) approaches and a Posterior Focussed Catch Reduction Approach (PFCRA) that produced complementary results. Using the SRA results, they concluded that in 2012 the longtail tuna stock—assumed for modelling purposes to be a single panmictic stock throughout the Indian Ocean—was subject to overfishing (F/F_{MSY} = 1.08) and was nearing an overfished state (B/B_{MSY} = 1.12).

Since this first assessment, the IOTC secretariat has conducted an updated stock assessment every year for longtail tuna in the Indian Ocean, but slightly refining the assessment models to cope with the generally poor catch and effort data available. Using an Optimised Catch-Only Method (OCOM), the stock continued to be subject to overfishing and in an overfished state in 2013 (F/F_{MSY} = 1.11; B/B_{MSY} = 1.02) (Martin and Sharma 2015), and subject to overfishing and in an overfished state in 2014 (F/F_{MSY} = 1.03; B/B_{MSY} = 0.99) (Martin and Robinson 2016). In the most recent assessment for 2015 using OCOM, Stochastic Stock Reduction Approaches (SSRA) and Catch-MSY (C-MSY) models, Martin and Fu (2017) showed that F/F_{MSY} and B/B_{MSY} have slightly reduced to around 1.0, due to a reduction in catches from 175,459 t in 2012 to 136,849 in 2015. However, considering the results from the three models, and the large uncertainty in parameter values, they concluded that the stock was still subject to overfishing and overfished.

Southeast Asia

Three assessments of longtail tuna have been conducted in Southeast Asia, where some of the most significant fisheries exist for the species, particularly for small fish (< 50 cm FL), presumably juveniles. An assessment conducted for Malaysian waters for the period 1998–1992 using a YPR analysis (Raja Bidin and Rumpet 1990) was based on landings from two adjacent landing sites in the southwest South China Sea and estimated an E of 0.630 year^{-1}. This value exceeded the estimated E_{MAX} value of 0.490 year^{-1}, indicating that the stock was most likely subject to overfishing.

Restiangsih and Hidayat (2018) used using a YPR model based on monthly length-frequency samples taken in the Java Sea during 2014 and estimated longtail tuna to have an F of 1.01 year^{-1} and an E of 0.62 year^{-1}. They also concluded that the stock was subject to overfishing, primarily due to high catches by gillnets that are most commonly used in the region.

The second stock assessment initiated by SEAFDEC for longtail tuna was undertaken by Nishida et al. (2016) for the South China Sea, and represents one of the more reliable assessments for the species. They used CPUE data in ASPIC models to characterise the stocks for 2014 and determined that the stock was exposed to extremely low fishing mortality (F = 0.193 year^{-1}), resulting in the stock not being subject to overfishing (F/F_{MSY} = 0.18) and was not overfished (B/B_{MSY} = 2.22). In a review of the model, Siriraksophon (2017) advocated for an increase in fishing effort, despite major uncertainties in the model resulting from the use of data only from Thai fisheries (mainly purse-seine).

Oceania

Only one stock assessment has been conducted for longtail tuna in Oceania—in Australian waters (Griffiths 2010)—that used an age-structured YPR model based on a combination of fish aged directly from their otoliths and length-frequency data. Therefore, the assessment is based on the most reliable biological data available and probably represents one of the most reliable assessments for the species. The assessment characterised the period 2004–2006 where the estimated average annual F and E was 0.24 year^{-1} and 0.353 year^{-1}, respectively. At this level of exploitation, the stock was not subject to overfishing relative to both F_{MAX} and $F_{0.1}$. However, when considering the spawning biomass, the current fishing mortality—where commercial exploitation is negligible by global standards—was in the vicinity of $F_{40\%}$, indicating that the stock was probably fully fished and that any increase in fishing effort would likely result in the stock being overfished. The assessment explored the potential benefits of increasing minimum retention lengths and handling practices to reduce post-release mortality to reduce fishing mortality by the recreational fishery, but these measures proved to provide marginal benefits to the stock since the majority of the catch was composed of large (> 60 cm FL) fish.

Discussion

Tunas are among the most productive and economically important fishes in the world's oceans, annually supplying over 4 million tonnes of product to domestic and export markets since 1998 (FAO 2019). For the species that comprise the majority of the world's capture production, namely skipjack and yellowfin tunas, the sustainability of their catches can be attributed to their biology—being short-lived (< 10 years), fast-growing, maturing early in life (< 2 years) and highly fecund—and their diffuse geographic distribution across ABNJ. In contrast, this review has shown longtail tuna to be relatively long-lived (up to 18 years), slow-growing, and have a geographical distribution that is confined to relatively shallow continental shelf waters that make them vulnerable to capture by a range of coastal fisheries. Consequently, longtail tuna form an increasingly important component of a range of artisanal, recreational, and small and industrial scale commercial fisheries in many countries throughout the species' geographic range. However, non-reporting, and misidentification or taxonomic aggregation of small tunas—e.g., "Tongkol" in Indonesia (Ingles et al. 2008) and "Shibi" in some regions of Japan (Itoh et al. 1996)—have contributed to limitations in accurately aligning catch data with consumer demand (Willette et al. 2017) and our current poor understanding of the true extent of fishing impacts on their stocks.

In the face of the declining spawning biomass of several economically important species of pelagic fisheries in the Indian Ocean since at least the 1990s, including bigeye tuna (Langley 2016a), yellowfin tuna (Langley 2015), albacore (Langley and Hoyle 2016), swordfish (Nishida and Yokoi 2017), blue marlin (Wang and Huang 2016) and striped marlin (Nishida 2015; Wang 2015)—and in some cases, overexploitation—longtail tuna and other neritic tuna and tuna-like species including kawakawa, frigate and bullet tunas and seerfishes have become an increasingly attractive alternative for the fisheries of coastal States.

Moreover, the increase in Somali piracy in the western Indian Ocean that resulted in a dramatic shift in the effort by large-scale commercial tuna fleets, such as drift gillnet fisheries of Iran and Pakistan, to fish coastal waters to target neritic species since at least 2009 (Al-Kiyumi et al. 2014, Moazzam 2014) is likely to have greatly exacerbated pressure on the Indian Ocean longtail tuna stock. Although Somali piracy appears to have abated in recent years, which has contributed to the re-establishment of more traditional tuna and billfish fishing grounds in ABNJ in the Arabian Sea (Moazzam and Ayub 2015; Nishida 2015), the extent to which the additional post-2009 effort has impacted the spawning stock of longtail tuna and the population's potential to recover whilst being exposed to current levels of fishing effort remains unknown.

Similar to the Indian Ocean, declines in the spawning biomass of target species in the WCPO have been well documented for yellowfin tuna (Tremblay-Boyer et al. 2017), bigeye tuna (McKechnie et al. 2017), swordfish (Takeuchi et al. 2017) and striped marlin (Davies et al. 2012) and pose a risk that fisheries may begin to increasingly target neritic tunas in order to remain profitable and provide food security for coastal States, particularly those bordering the South China Sea. There is certainly growing evidence of the increased retention of formerly discarded species (e.g., wahoo, rainbow runner, dolphinfish) with the increasing shift by the WCPO industrial purse-seine fishery to set on floating objects (i.e., FADs), which attract high diversity and biomass of tunas, sharks and tuna-like species (Leroy et al. 2013, Griffiths et al. 2019a). It is possible at some point that coastal States throughout Southeast Asia may begin to withdraw their industrial vessels from the current distant water purse-seine and longline fishing grounds located in the western Pacific Warm Pool Province (Williams and Reid 2018) to target longtail tuna and other neritic tunas and tuna-like species within more local waters, such as the South China Sea.

Despite the widespread adoption of the principals of the precautionary approach to fisheries management (FAO 1995) by numerous national fisheries agencies worldwide and the more recent pursuit of more holistic ecosystem-based approaches to fisheries management (FAO 2003) by RFBs such as the Asia–Pacific Fishery Commission (FAO 2017a), it is worrisome that such obvious increases in longtail tuna catches have failed to capture the attention of fishery managers until very recent years, particularly in the Indian Ocean. Although many aspects of the biology, movements and stock structure of longtail tuna are little understood, this review has demonstrated there is certainly sufficient information available to undertake reasonably rigorous integrated assessments—beyond that of simplistic YPR models—for at least each of the four putative stocks (Fig. 2) using new data-poor assessment methods that have been applied recently to the Indian Ocean stock (see Martin and Fu 2017).

Even more alarming is that several independent lines of evidence, albeit from rudimentary YPR models based on biological and fishery data of varying degrees of reliability, have indicated that longtail tuna has likely been subject to overfishing and overfished for a number of decades, especially where intense and poorly regulated fisheries exist. For example, even as far back as the late 1980s in Omani waters where the most reliable biological and fishery data was available for longtail tuna at the time, Prabhakar and Dudley (1989) warned that the stock was probably fully exploited and recommended no further increase in fishing effort. Unfortunately, some 30 years later, such scientific advice has not yet initiated the development or implementation of meaningful CMMs, neither within the coastal States or at the level of RFMO.

Developing a management framework

The fisheries management frameworks in place across the distribution of longtail tuna differ markedly, and have probably contributed to the slow progress in the species being formally recognised as requiring specific CMMs. At a macro level, different management arrangements are in place in the Indian Ocean versus the Western Pacific Ocean as the Indian Ocean has a single organisation—the IOTC—that has ultimate management responsibility for longtail tuna. Based on evidence of overexploitation of longtail tuna from recent exploratory stock assessments undertaken annually by the IOTC Secretariat between 2013–2017, there is an immediate opportunity for the IOTC to promulgate CMMs aimed at reducing pressure on the species. However, CMMs developed by the IOTC that may afford some protection to longtail tuna, either directly or indirectly, only become mandates for those members that agree to a CMM at the time of its adoption by the Commission. Therefore, this would require the countries that contribute most to catches to agree on measures to reduce fishing effort, especially amongst the gillnet fleets. Each nation should move to prepare a comprehensive management plan for these fleets, which set out management objectives, licencing controls, catch limits, consultation arrangements, monitoring/control/enforcement measures and catch monitoring in accordance with both established best practices and the requirements of any agreed CMM (Cochrane 2002; FAO 2003; Cochrane and Garcia 2009).

Fortunately, the recent stock assessment outcomes have generated the impetus for the IOTC Scientific Committee in 2017 to recommend the introduction of CMMs for longtail tuna; including the development of limit reference points and the reduction in catches by 10% of 2015 levels (to 136,849 t) to not exceed a provisional MSY of 140,000 t (IOTC 2017). Although this is a positive move forward to develop interim precautionary management measures, these recommendations have not yet been accepted and implemented into formal CMMs by the IOTC.

Another positive initiative by the IOTC that should benefit longtail tuna was the development of a CMM (Resolution 17/07 "On the prohibition to use large-scale driftnets in the IOTC area") that entered into force in 2017, prohibiting the use of large-scale drift gillnets (> 2.5 km in length) in the IOTC area of competence by 2022. This measure is likely to reduce the fishing mortality on longtail tuna, as well as other neritic tunas and a range of bycatch species with vulnerable life histories, including turtles, cetaceans, and elasmobranchs (Northridge 1991; Moazzam and Nawaz 2014). Additionally, although there is no specific CMM in place for longtail tuna in Pakistan, there is a two-month closure (June–July) that provides some respite for the longtail tuna stock. During the winter (January–March) the Pakistan gillnet fleet moves to offshore waters of the EEZ and in ABNJ, and thus longtail tuna are not harvested during this period.

In contrast to the IOTC, longtail tuna is not an explicit responsibility of the Western and Central Pacific Fisheries Commission (WCPFC), since its Convention includes only "highly migratory species" listed under Annex I of the 1982 United Nations Convention on the Law of the Sea (UNCLOS) (UN 1982), which does not include longtail tuna. A further complication is that the WCPFC Convention area does not include the waters throughout Southeast Asia and the South China Sea (see Annex 4 of SPFFA 2000), where the majority of longtail tuna catches are made outside of the Indian Ocean. However, FAO catch statistics attribute longtail tuna catches to Major

Fishing Areas 61 and 71 that encapsulate a large proportion of the WCPFC Convention area. Fortunately, RFBs within Southeast Asia and the South China Sea are beginning to make progress to improve knowledge on the biology and fisheries for longtail tuna, mostly as part of a wider complex of neritic tunas and seerfishes. For example, in 2014 SEAFDEC established the Scientific Working Group on Neritic Tuna Stock Assessment in the Southeast Asian Waters and subsequently developed the RPOA-Neritic Tunas in the ASEAN (Association of Southeast Asian Nations) Region in 2015 (SEAFDEC 2017).

The RPOA-Neritic Tunas has focused on data collection, with work plans being established for research, catch monitoring, and capacity building for Member States, which should greatly improve the quality of data available to undertake future assessment of the important Southeast Asian longtail tuna stock(s).

The earliest known management initiative in the WCPO was the ban on commercial targeting of longtail tuna as part of its declaration as a "recreational only" species in Australian waters in 2006 (Borthwick 2012). This was essentially implemented to prevent any future large-scale commercial targeting of longtail tuna, where there has been negligible commercial exploitation historically.

The growing interest in management has resulted in the development of fisheries management plans that cover longtail tuna in both Thailand and Indonesia. In 2015, Thailand implemented a new fisheries management plan that includes all pelagic species (DOF 2015), which is a valuable step forward. The Thai plan aims to regulate overall fishing effort rather than seek to implement a large number of individual species management measures. Whether this will benefit longtail tuna has not yet been demonstrated. Indonesia's tuna plan (2014–2019) (MAFRI 2015) is detailed but in terms of the neritic tunas, is mainly focused on data gathering rather than putting into place effective management controls. Part of the reason for this may be the optimistic stock assessment but history would suggest that the best time to put in place catch controls is when stocks are healthy.

However, even if all countries had management plans in place there would continue to be a need for coordination across countries in order to keep the cumulative fishing mortality at a biologically sustainable level. Therefore, the largest challenge in the western Pacific is that there is no fishery body that has responsibility for coordinating management across the countries that catch longtail tuna. Moreover, there seems to be a current dispute amongst ASEAN members as to where responsibility for initiatives on neritic tunas should lie (SEAFDEC 2018). To date there has been little political appetite across the various smaller RFBs to commit the required resources to initiate a comprehensive research program and stock assessments for longtail tuna in the western Pacific Ocean, despite catches throughout Southeast Asia contributing 56% to the global catch of longtail tuna in 2017 (FAO 2019). Much of the current funding has been sourced from foreign aid (e.g. via the Swedish International Development Cooperation Agency). The management of longtail tuna—despite attempts to push for multijurisdictional management approaches—has to compete with a plethora of issues confronting Southeast Asian nations such slave labour (Marschke and Vandergeest 2016; Fischman 2017) and IUU fishing (Li and Amer 2015).

The aforementioned complexities mean there is no clear mechanism for establishing CMMs that parallel those available in the IOTC. Given the large-scale movements of longtail tuna, there may be merit in seeking a change to the relevant articles of the WCPFC Convention or inclusion of the species in Annex I of UNCLOS that underpins the WCPFC Convention. However, under Article 5 of the WCPFC Convention it states the Commission will "assess the impacts of fishing, other human activities and environmental factors on target stocks, non-target species, and species belonging to the same ecosystem or dependent upon or associated with the target stocks". Therefore, it stands to reason that the WCPFC should assume responsibility for longtail tuna as they belong to the same ecosystem, and are associated with, several exploited species listed under Annex 1, in particular *E. affinis*. *A. thazard* and *A. rochei*. It should also be noted that the absence of particular species in Annex 1 has not precluded the WCPFC from developing specific CMMs for some of these species, such as sea turtles (CMM 2008-03).

Alternatively, a specific management body for neritic tunas could be developed, possibly via the ASEAN. Such an approach has been used in the western Indian Ocean, where the Regional Commission for Fisheries (RECOFI) developed a Working Group on Fisheries Management in 2001, which is currently developing improved data reporting and data harmonization among its Member States, and plans to coordinate stock assessments on the region's most economically important neritic species, such as Kingfish (*S. commerson*) (FAO 2017b). Nonetheless, the aforementioned approaches are unlikely to result in suitable catch controls being developed in a timely manner to curb the overexploitation of longtail tuna in recent years.

Research and management priorities

Longtail tuna has attracted the attention of scientists at least since the work of Serventy (1942b), but there has been surprisingly little research conducted in the intervening 76 years, and much of the work appears to have been undertaken in an opportunistic or *ad hoc* manner, or using methodologies or sampling designs that are not of sufficient reliability to characterise population dynamics parameters to be informative for stock assessment. Much of the reasoning for this is twofold. First, many of the countries that contribute to the global capture production of longtail tuna are developing nations, and therefore do not have the resources to undertake the required biological research and fisheries monitoring or employ adequately trained staff to undertake these activities. Second, until the late 1980s, longtail tuna had not been established as a bona fide species of economic or social importance, as its magnitude of catches were generally dwarfed by catches of principal species such as skipjack and yellowfin tunas, especially in the WCPO. While managers have directed their attention, and often limited resources, to rectify the situations for principal target species, longtail tuna appears to have been overlooked, until recent scientific evidence has shown that the species is slow-growing and long-lived (living for at least 18 years)—similar to the life histories of the larger *Thunnus* species bigeye and southern bluefin tunas that have contributed to their overexploitation (Griffiths et al. 2010a)—and is now in an overexploited state throughout the majority of its worldwide distribution.

Fisheries scientists and resource managers must recognise that urgent action is required to ensure the long-term sustainability of longtail tuna stocks. In order to make meaningful progress in better understanding the population dynamics of longtail tuna and their fisheries to improve the reliability of stock status determined by stock assessment models, a number of fundamental studies are recommended and discussed hereafter to be undertaken in at least the four major putative stocks of longtail tuna (Fig. 2). Until such times as more reliable data become available to better assess longtail tuna stocks, precautionary management measures need to be exercised, such as setting interim input and/or output control measures such as introducing or reducing quotas or fleet capacity (e.g. IOTC 2017), or changing gear configurations, such as increasing mesh size of nets to reduce the mortality on juvenile tuna.

Improved quality and reporting of catch and effort for conservation and management

As has been discussed throughout this review, our poor level of understanding of longtail tuna population dynamics, fisheries exploitation and stock status primarily stems from the historically lower catches and economic importance of longtail tuna, compared to principal target species, that has failed to garner sufficient interest from national fisheries agencies, RFBs and RFMOs to invest resources into monitoring and research. Although the tuna catch composition has certainly changed in recent years, particularly in the Indian Ocean, a major obstacle for data collection is that a large proportion of the longtail catch is derived from small-scale commercial and artisanal fisheries—and primarily recreational fisheries in Australia. Quantifying catch and effort from these fisheries can be an enormous challenge as there can be large numbers of operational vessels, but many do not need to be registered or require a fishing licence or permit—or at least appear on any type of official registration list—or require their catch and/or effort to be reported (e.g. Somalia; Persson et al. 2015). Consequently, the magnitude of participants in these fisheries and their impacts on stocks are poorly understood. Even fishery-independent surveys of these fleets are logistically difficult and often cost-prohibitive as vessels or fishers need to be intercepted at an enormous number of diverse access points (e.g. public and private docks, beaches, rivers, motherships) that are dispersed across thousands of kilometres of coastline and open ocean (Griffiths et al. 2010b; Geehan 2016).

It is of paramount importance that coastal States, with the support of RFBs and RFMOs, develop, or improve, data collection systems that are reliable and validated periodically. In Indonesia for example, data collection systems have been in place since the 1970s and comprise obligatory reporting from fishing companies, monitoring at landing sites, and periodic fishery-independent surveys of fishing villages.

Recent advances in, and broader availability of, molecular genetic methods present new opportunities to rapidly and accurately examine fish stocks and catches (Willette et al. 2014). DNA barcoding is an increasingly common method used in both developed and developing countries to detect mislabelling of market-sold tuna (Maralit et al. 2013, Abdullah and Rehbein 2014; Khaksar et al. 2015), and has recently been shown effective in assessing the biodiversity and biomass of marine fish, including tuna, in seawater samples (Takahara et al. 2012, Kelly et al. 2014, Port et al. 2016, Willette 2017). Of particular value is a pair of *Thunnus*-specific primers (MiFish-tuna-F and MiFish-tuna-R), which can unambiguously distinguish longtail tuna from other *Thunnus* species (Miya et al. 2015). This may be one plausible validation process that may be periodically applied to ensure correct species reporting, or at the least, better allow the extent of misidentification to be understood and corrected for in final catch statistics.

Although improved data collection processes will greatly improve the quality of catch and effort data for fisheries that catch longtail tuna, it is clear, even from the limited data currently available, that implementation of management measures aimed at controlling catches is needed. Capacity reductions, for example, may not only benefit longtail tuna but other species known to be under pressure (e.g. yellowfin tuna). Moreover, as stocks of some principal species decline fishing effort is likely to shift to other species, such as longtail tuna, which may result in serial depletion of new target species, and ultimately the degradation of the structure and function of the ecosystem. In the South China Sea, the focus needs to be on developing a more robust mechanism for agreeing and implementing coordinated management across jurisdictions. This could take place in the absence of any formal RFMO, if the political will is sufficient.

Markets and market demand

There is currently insufficient information on the usages of longtail tuna and, in particular, their international trade and the markets they feed into. Understanding the trade can help generate a better understanding of volumes, especially in the context of growing trade requirements for more accurate traceability. Importing countries, such as the United States, can impose data collection requirements on exporting nations if traceability is unclear or if the fishery in question is in violation of other requirements such as the Marine Mammal Protection Act of 1972. In January 2017, the United States introduced the Seafood Import Monitoring Program (SIMP) that requires data on fish products to be verified at each step in the supply chain from harvest to final importation into the US (Willette and Cheng 2018).

The gillnet fisheries for tunas in Iran and Pakistan would be among the most affected under the SIMP, which would also apply to intermediary nations that may be importing and processing longtail tuna products prior to arrival into the US. The SIMP gives exporting nations a 5-year period to demonstrate to the US government that they have a fishery-level marine mammal bycatch that is no different from a comparable US fishery. Failure to provide this assurance will result in the products being denied entry to the US.

Stock structure and movement

The definition of stock boundaries is critically important in the assessment of species impacted by fishing (Cadrin and Secor 2009). Stock boundaries have been defined using a variety of techniques including morphometrics (Serventy 1956; Abdulhaleem 1989), conventional tagging and biological markers (e.g., parasites, otolith microchemistry) (Begg and Waldman 1999), and mtDNA D-loop genetic analysis (Willette et al. 2016). However, each of these methods infer potential stock boundaries across different time scales from days to months (tagging), years (otoliths), to generations (morphometrics and genetics).

Genetics has become an increasingly powerful and inexpensive method used to define stock structure for tunas, particularly single nucleotide polymorphism (SNP) markers (Grewe et al. 2015). Genetic analyses are ideal in situations where a strong genetic gradient can be used to differentiate stocks. However, minimal generational gene flow between true sub-populations can result in the appearance of a single panmictic stock. Therefore, stock structure studies for longtail tuna may benefit from the use of complementary techniques used in concert (see Begg and Waldman 1999), such as genetics to establish an evolutionary scale baseline coupled with, for example, conventional tagging that will allow the shorter term direction and magnitude of movement of fish to be determined in order to identify independent reproductive stocks.

Such work would involve the collection and tagging of specimens at sufficient spatial scales across the entire distribution of the stock, for example the entire Indian Ocean. With the rapid advancement of genetic techniques, a genetic study may serve two important purposes. First, it can define stock boundaries, and the second may be to use genetic material for new cost-effective close-kin mark-recapture techniques (Bravington et al. 2016b) to estimate the absolute abundance of longtail tuna for stock assessment, which has been achieved for southern bluefin tuna (Bravington et al. 2016a) and the white shark (Hillary et al. 2018). Such an estimate of abundance would greatly reduce the current uncertainty in stock size and the estimated level at which the stock can be sustainably harvested using biological reference points such as MSY (see Martin and Fu 2017).

Growth and reproductive dynamics

As shown in Tables 2 and 3, there are wide-ranging estimates of growth and reproductive parameters for longtail tuna, even within the same region, which is likely a result of inadequate sampling and/or unreliable analysis techniques (e.g. modal length analysis). These effects can have significant impacts on estimates of growth and mortality parameters, and thus, stock status. Although population parameters and stock status can be estimated reliably using length-frequency data, as is routinely done using MULTIFAN-CL for principal tuna species in the WCPO (Fournier et al. 1998), these models require a great deal of data from all fleets and time and spatial strata, which is unlikely to be feasible for several coastal States throughout Southeast Asia and the Indian Ocean where resources for long-term monitoring may be limited.

With respect to reproductive dynamics, macroscopic staging and gonadosomatic indices have been used in the majority of published studies over reasonably inexpensive histological methods, which have far higher precision for estimating L_{50} and developing maturity at length (or age) ogives (Vitale et al. 2006, Ferreri et al. 2009) and allowing the identification of spawning locations using the presence of post-ovulatory follicles in the ovaries.

Therefore, it is recommended that growth and reproductive studies be undertaken within each stock using, at a minimum, routine methodologies applied to samples representing the entire size spectrum of fish found within each stock. For ageing studies, this should involve the analysis and quantification of daily and/or annual growth increments in sectioned sagittal otoliths that have been validated by chemically-marked (e.g., oxytetracycline, bomb radiocarbon) fish, or at least by otolith edge-type analysis, of fish representing a wide range of age classes (Campana 2001). Reproductive studies ideally should be undertaken simultaneously with growth studies using the same sampled fish, thus optimising cost-effectiveness of the sampling. If pilot studies or previous work cannot determine the spawning period, monthly histological samples should be processed, or a GSI be closely monitored, to detect changes in reproductive condition. Intensive sampling is then recommended during the spawning period across the widest possible size range of fish in order to optimise the precision of an L_{50} estimate and representativeness of the maturity ogive.

If stocks were to be prioritised for this biological research, we suggest to first examine the Indian Ocean stocks, since this is the region that contributes most to the global catch of longtail tuna and where the stock is overfished and overfishing is known to be occurring.

Given that the putative stocks of longtail tuna straddle several political boundaries of varying spatial scales from coastal States, to RFBs, to RFMOs (Fig. 2), it is imperative that entities responsible for the management of a particular stock(s) of longtail tuna closely collaborate to ensure consistency in collection and analysis methods, which may be achieved through forums such as the IOTC's WPNT, RECOFI's Working Group on Fisheries Management (WGFM), and SEAFDEC's RPOA-Neritic Tunas. Improved data quality will allow more reliable stock assessments to be undertaken and allow fishery managers to be better equipped to develop appropriate CMMs to safeguard the long-term sustainability of longtail tuna stocks.

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