IOTC-2016-WPTT18-37
Received: 21 October 2016

Sex-ratio, size at maturity, spawning period and fecundity of bigeye tuna (*Thunnus obesus*) in the western Indian Ocean.

[1,2]Zudaire I., [1]Chassot E., [2]Murua H., [1,5]Dhurmeea Z., [4]Cedras M., [1]Bodin N.
[1] IRD - research unit MARine Biodiversity, Exploitation & Conservation (MARBEC), Victoria, Mahé, Seychelles
[2]IKERBASQUE, Basque fondation for science, Bilbao, Spain.
[3]AZTI-Tecnalia, Portu aldea s/n, Pasaia, Spain.
[4]Seychelles Fishing Authority (SFA), Victoria, Mahé, Seychelles
[5]Department of Biosciences, Faculty of Science, University of Mauritius, Réduit, Mauritius

Abstract

Opportunistic sampling of bigeye tuna (*Thunnus obesus*; BET) was conducted in the western Indian Ocean from 2010 to 2015 to study important reproductive traits (i.e., sex-ratio, size at maturity, spawning season and fecundity) with the aim to provide reliable information to improve the stock assessment. Overall 507 BET were sampled (including 204 females, 216 males and 87 indeterminate fishes) from which 158 ovaries were analyzed histologically. Significant bias towards females was found in the sex ratio of small individuals while males appeared dominant at large sizes. High reproductive activity was observed from January to March. The size at which 50% of females reach maturity (L_{50}) was estimated at 102±4.5 cm fork length (L_F), setting maturity threshold at primary vitellogenic oocyte stage. Mean batch fecundity (F_B) was estimated at 0.75±0.52 million oocytes and mean relative batch fecundity (F_{Brel}) at 11.54±7.11 oocytes per gram of fish weight. No significant relationship between fecundity (F_B and F_{Brel}) and size (L_F) was found.

Keywords:
Size at maturity / Sex ratio / Spawning/ Bigeye Tuna/ Indian Ocean/ Fecundity

1. Introduction

Bigeye tuna (*Thunnus obesus*; BET) is a cosmopolitan large pelagic tuna species inhabiting tropical and subtropical waters (Collette and Nauen 1983). It is the third tuna target species worldwide corresponding to ~9% of total tuna catches and representing a global catch of about 440,000 t over the last decade. In the Indian Ocean (IO), annual bigeye catches were about 100,000 tonnes in the recent period. BET is a valuable meat for the sashimi market, with it's a commercial value increased during the past decades. With 56% of total annual catches, Indonesian and Taiwanese longline (LL) fisheries are the principal fisheries harvesting BET in western IO (ISSF, 2016). However, the high piracy activity in the region during 2008-2012 has induced a decline in LL activity and catches of this species have dropped since the mid-2000s (Langley et al. 2013). Purse seine (PS) fleet, with 28% of BET total annual catches, is the second fishery in the area and its activity contrary to LL has kept relatively stable since 2000. In the last BET stock assessment conducted in 2013 by the Indian Ocean Tuna Commission (IOTC), it was reported that the population was not overfished (Langley et al. 2013). However, in recent years, the IOTC Scientific Committee concluded BET stock may have been fully exploited and recommended the implementation of a reduction in catches of BET from all gears as soon as possible (IOTC 2015).

Biological information on maturity, fecundity, and spawning season and location have been identified by the Working Party on Tropical Tunas as high priority to the stock assessment (IOTC 2015). Acquiring knowledge on these reproductive parameters improves the understanding of the fluctuations in the population dynamic and hence, it allows to better assess population resilience to fishing and environmental changes (Murua and Motos 2006; Morgan et al. 2009). However, information on BET reproduction is still scarce (Juan-Jordá et al. 2013) and most of the efforts on this aspect have been conducted in the Pacific Ocean (Farley et al. 2003; Schaefer et al. 2005; Farley et al. 2006; Zhu et al. 2010; Sun et al. 2013). In the Indian Ocean, the analysis of important reproductive traits has remained preliminary and little information is available regarding sex-ratio, size at maturity and fecundity (Stéquert and Marsac 1989; Stobberup et al. 1998; Nootmorn 2004; Ariz et al. 2006; Zhu et al. 2011). Thus, the objective of this work is to contribute increasing knowledge on reproduction of BET by providing reliable information on important reproductive traits (i.e., sex-ratio, size at maturity, spawning period and fecundity) which are involved in the reproductive potential of this tuna species.

2. Material and methods

2.1. Field sampling

Bigeye tuna (n = 507; females = 204 and males = 216) was sampled from 2010 to 2015 in an opportunistic sampling at processing factories of Seychelles and Mauritius. Individuals were caught by purse-seine fleet operating in the Western IO (Figure 1). Fork length (L_F, cm), first dorsal length (L_{FD}, cm), thorax length (L_T, cm) and total weight (W_T, Kg) were recorded from each fish. The gonads were then excised and the total weight (W_G, g) recorded. Gonadosomatic index (GSI) was calculated as $GSI=W_G/W_T \times 10^2$. A cross section of gonads of 4–5 cm was cut between the middle and end part of the right or left lobe and preserved in 4% buffered formaldehyde for reproductive analysis. Information regarding fishing date and area was obtained from vessels logbooks and plans of brine-freezing wells through close collaboration with the EU purse seine fleet and factories.

2.2. Length-weight relationship and sex-ratio

Multiple linear regression model was applied on the overall sampled BET (males and females) to assess the variability observed in weight as the function of length and sex. Sex ratio (SR) was calculated as the proportion of females by 5 cm L_F classes, and Chi square test was used to examine differences from an expected 1:1 by size class as $SR= N_f /N_t \times 10^2$ where N_f is the number of females and N_t is the total number of sampled fish.

2.3. Reproductive analysis

A 1-cm cross-section from the preserved portion of each ovary was embedded in paraffin, sectioned at 5-7 µm and stained with Hematoxyline and Eosin. Ovaries were classified according to the most advanced oocyte stage present based on Zudaire et al. (2013a): (i) immature phase (P_I) which includes oocytes in the primary growth stage ; (ii) developing phase (P_D) which includes oocytes in the stages of cortical alveoli (CA) and primary (Vtg1) and secondary vitellogenesis (Vtg2); (iii) spawning-capable phase (P_{SC}) which includes oocytes in the stages of tertiary vitellogenesis (Vtg3), germinal vesicle migration (GVM), germinal vesicle breakdown (GVBD), and hydration (Hyd); (iv) regressing phase (P_{RG}); and (v) regenerating phase (P_R) characterized by the presence of maturity makers, late-stage atresia and a thicker ovarian wall than seen in immature fish. The atretic condition to appraise the P_{RG} was based on Hunter and Macewicz (1985) and the classification for atresia stages described in Zudaire et al. (2013a). However, the estimation of atresia for ovaries collected at the cannery entails difficulties due to their exposure to the brine conservation process used in PS. This conservation method produces breakages in the follicle wall and chorion and makes difficult the identification of different cytoplasm structures, hence, precise quantification of atresia was not always possible. No postovulatory follicles were found in the ovaries.

2.4. Size at maturity (L_{50})

Size at which 50% of the population reach maturity (L_{50}), was calculated by fitting the proportion of mature females (identified through histological analysis) by 10 cm L_F classes to a logistic equation

(Ashton, 1972): $P_{\mathrm{mature}} = e^{\alpha+\beta L_F}/1+e^{\alpha+\beta L_F}$ with P_{mature} as predicted proportion of mature females; L_F in cm; α and β as coefficients of the logistic equation. The L_{50} was estimated as the ratio of the coefficients ($-\alpha$ x β^{-1}). A binomial distribution with logit link function was used to fit the above equation to the data. The maturity curve was fitted to the data on the basis of three different assumptions regarding female maturity threshold: (i) ovaries with oocytes at the CA stage onward (Brown-Peterson et al. 2011), (ii) ovaries with oocytes at Vtg1 stage onward, and (iii) ovaries with oocytes at Vtg3 stage onward were considered mature (Schaefer 1998; Zhu et al. 2008).

2.5. Batch fecundity and relative batch fecundity

Batch fecundity (F_B), i.e., the total number of oocytes released per batch, was estimated for 25 ovaries by gravimetric method (Hunter et al. 1985), counting the oocytes at the most advanced stage of development present in actively spawning capable sub-phase ovaries (i.e. ovaries with oocytes at GVM, GVBD and Hyd stages). Homogeneity in oocyte density among whole ovary was assumed on the basis of previous works on tuna (Stéquert and Ramcharrun 1996). For F_B analyses, three subsamples of 0.1 g (±0.01) were collected from each ovary. Each subsample was saturated with glycerin and oocytes were counted under a stereomicroscope (Schaefer 1998). F_B was calculated as the weighted mean density of the three subsamples multiplied by W_G. A threshold of 15% for the coefficient of variance was applied for the three subsamples, and when this threshold was surpassed, more subsamples were counted until this value was reached. Relative batch fecundity (F_{Brel}) was estimated dividing the F_B by fish gonad-free weight (i.e., $W_T - W_G$). Linear regression was used to investigate the relationship between F_B and F_{Brel} and biological parameters like L_F and W_G.

3. Results

3.1. Length-weight relationships and sex ratio

From the total of 507 bigeye tuna sampled, 410 specimens were used for the length-weight relationship analysis; 213 males ranged in size from 38 to 171 cm L_F and 197 females ranged from 47 to 174 cm L_F. The results for combined values of both sexes indicated a length-weight curve that differs from the IOTC official one (Fig 2). Sex did not significantly affect the relationship between L_F and W_T (p-value =0.121).

Sex ratio was analyzed by 5-cm size classes. A significant bias towards females was reported at small size classes (Table 1; L_F classes 95-100 cm). At intermediate and large size classes, no significant difference was found between sex although females were found to be more abundant at intermediate sizes (L_F 120-125 and 130-135 cm) while males started to become dominant at large sizes (Table 1; L_F > 150 cm) (Fig. 3).

3.2. Reproductive analysis and spawning season

According to the classification summarized in Table 2, 13.2% of females were at the P_I, 19.1% were at P_D, 18.4% were at P_{SC}, 25% at P_{RG} and 24.3% of the fishes showed ovaries at P_R. The 87% of sampled females were mature when maturity threshold was set at CA oocyte development stage. Monthly assessment of the ovary development, described high spawning activity from January to March when ovaries were found more developed with high percentage of spawning females, especially in February with 75% of studied population at P_{SC}. In contrast, from April to October, no spawning activity was observed among females and most ovaries analyzed during this period were less developed, with high proportion of immature individuals (Fig 4). P_R and P_{RG} females were found all over the year showing high variability between months (from 12 to 50% and from 16 to 50% of the population, respectively). Highest values of P_{RG} individuals were found in May (50%), while for P_R the highest percentages (50%) were reported in August and December. The monthly mean GSI values also described a period of high reproductive activity from January (0.63±0.32) to March (0.75±0.35) with maximum values in February (1.77±0.84) (Fig. 5). Afterwards, from April (0.23±0.16) to December (0.48±0.24), the GSI decreased and kept low.

3.3. Size at maturity

L_{50} was estimated at 88±4 cm L_F when females with ovaries at CA stage and onward were considered mature. This estimation increased to 102±4 cm L_F when Vtg1 was applied as maturity threshold and to 115±5 cm L_F when Vtg3 was applied (Fig 6).

3.4. Batch fecundity and relative batch fecundity

The estimated mean F_B was 0.75±0.52 million oocytes and varied from 2 to 0.13 million oocytes. The mean F_{Brel} was estimated at 11.54±7.11 oocytes per gram of gonad-free fish weight and fluctuated from 2.24 to 25.82 oocytes. No significant relationship (p-value > 0.05) was found between F_B and F_{Brel} with L_F. In contrast, significant relationship (p-value < 0.01) was found between F_B and F_{Brel} with W_G.

Spawning females were found only from January to March. Most of them were sampled in March, i.e. 83% of the females. F_B was highly variable between months and no seasonal pattern was observed in spawning dynamics. The maximum mean F_B value was found in February (1.03±0.54 million) and the minimum in January (0.4±0.13 million). Analysis of variance (ANOVA) performed on F_B and F_{Brel} by month did not reveal any significant temporal differences at a 95% confidence level (ANOVA; $F_{(2,21)}$=0.706, P=0.505; $F_{(2,21)}$=2.3, P=0.125 respectively; Fig 7).

4. Discussion

4.1. Sex ratio

Although the small sample size for some of the size classes might weaken the overall interpretation of the results, in the present study a significant difference on the sex ratio by length class was found at small size BET, dominated by females as previously reported for eastern (Nootmorn 2004) and southwestern IO (Ariz et al. 2006). However, at large sizes individuals (L_F >155 cm), a higher proportion of males was found among the studied population which is in accordance with previous studies in the Indian (Nootmorn 2004), Pacific (Kume and Joseph 1966; Schaefer et al. 2005; Sun et al. 2013) and Atlantic Ocean (Pallares et al. 1998). Two are more likely the explanations for the sex ratio bias: (i) different sex-specific growth rate and (ii) different sex-specific natural mortality (Sun et al. 2013). Kume and Joseph (1966) reported males' higher length frequency in Pacific Ocean and more recently, further evidences of sexual dimorphism in tuna growth has been reported in *Thunnus albacares* in the IO (Eveson et al. 2015) and *Thunnus alalunga* in Pacific Ocean (Williams et al. 2012), with males reaching larger sizes than females. Considering sexual dimorphism in population dynamics might modify the outputs of stock assessment and eventually the stock status (Tsai et al. 2014). Data on sex ratio should be routinely collected for BET to complement our study and validate the hypothesis of increasing proportion of males in the population at large sizes.

4.2. Reproductive analysis and spawning season

The sampling coverage of BET gonads by month in the present study was inadequate for a comprehensive description of the temporal pattern in spawning in the western IO. However, this is the first study using histological analysis of BET ovaries in the region, and some preliminary results derived from these data can be used to describe the reproductive activity of this species. Results described a spawning period from January to March, with high proportion of spawning individuals. Estimated mean GSI values also support described reproductive activity and it is in accordance with the period previously identified in the western (Stéquert and Marsac 1989; Nootmorn 2004) and eastern IO (Fourth and first quarter of the year; Stobberup et al. 1998). The high proportion of females at P_{RG} and P_R, especially in March, is particularly noticeable. It suggests that spawning activity is already finished in March for part of the population, although some active females can be observed as a result of the reproduction asynchrony at the population level. From April to October P_I, P_{RG} and P_R individuals are dominant describing a period at which reproductive activity at the population is low.

4.3. Size at maturity

In the current study, three different L_{50} estimates were provided derived from the three maturity thresholds applied on data (i.e., CA L_{50} = 88±4 cm L_F, Vtg1 L_{50} = 102±4 cm L_F and Vtg3 L_{50} = 115±5 cm L_F). L_{50} has been widely reported in the Pacific Ocean, applying different maturity classification methods (i.e., macroscopic and histological analysis) and statistical models, which have led to a wide range of L_{50} values from 102 to 135 cm L_F (Schaefer et al. 2005; Farley et al. 2006; Zhu et al. 2011; Sun et al. 2013). The lack of a standardized methodology used in previous studies, however, makes difficult comparison of this important reproductive trait between regions and oceans (Sun et al. 2013). It is well recognized that histological identification of ovaries is the best method to accurately identify the oocyte development stages and hence to properly estimate size at maturity (Schaefer 2001). In the Indian Ocean, previous L_{50} estimations for BET were carried out by macroscopic identification of gonads reporting L_{50} at 88 cm L_F (Nootmorn 2004) and 119 cm L_F (Zhu et al. 2011). In the current study, applying histological analysis, L_{50} has been provided when maturity threshold is set at CA (Zudaire et al. 2013b; Grande et al. 2014). According to Brown-Peterson et al. (2011), an individual is considered mature when oocytes enter into CA stage. However, most of the previous tuna L_{50} estimations through histology have used vitellogenic stage of oocyte to fix maturity threshold (Schaefer et al. 2005; Sun et al. 2013). In the current work, both estimations applying Vtg1 and Vtg3 (L_{50} = 102 cm L_F and L_{50} = 115 cm L_F, respectively) were into the ranged reported in the western Pacific Ocean (102 cm L_F; Sun et al. 2013) and eastern and central Pacific Ocean (135 cm L_F; Schaefer 2005).

4.4. Batch fecundity and relative batch fecundity

To our knowledge, our analysis provides for the first time an estimation of F_B and F_{Brel} for BET in the western IO. The observed mean F_B (0.76 million oocytes) and F_{Brel} (11.54 oocytes per gram of body) are much lower than those reported in the eastern central Pacific (1.45 million oocytes and 24 oocytes per gram of body; Schaefer 2005) and western Pacific Ocean (3.06 million oocytes and 56.12 oocytes per gram of body; Sun et al. 2013). Besides a possible effect of the ocean-base variability, the fact that most of the analyzed individuals (83%) for fecundity were caught in March, close to the end of the reproductive season, is a factor that could underestimated our estimates of fecundity (Farley et al. 2013). Thus, an increase of the sampling coverage, from December to March, is required for a comprehensive description of the spatiotemporal dynamic in reproductive potential of BET in the western IO.

In the current study, F_B and F_{Brel} were not related significantly to L_F and W_T, in contrast to previously reported in the Pacific Ocean (Schaefer et al. 2005; Sun et al. 2013). F_{Brel} appeared highly variable with L_F, and a negative relationship was predicted. This pattern may suggest lower reproductive investment at large individuals, however, further analysis is required to better study size specific fecundity in BET in the western IO.

Acknowledgements

We are grateful to all staff of «Mauritius cannery» for helpful assistance during sampling operations. The work was partially funded by IRD and the European Data Collection Framework (DCF, Reg 199/2008 and 665/2008). IZ was funded through the Postdoctoral Program of the Basque Government. This work also benefited from the French ANR-funded project EMOTION (ANR JSV7 007 01).

References

Ariz J, de Molina AD, Ramos ML, Santana JC (2006) Bigeye tuna and yellowfin tuna sex-ratio analysis from observer data obtained during the experimental cruise on Spanish longliners in the Southwestern Indian Ocean in.

Brown-Peterson NJ, Wyanski DM, Saborido-Rey F, et al (2011) A standardized terminology for describing reproductive development in fishes. Mar Coast Fish 3:52–70.

Collette BB, Nauen CE (1983) FAO species catalogue, Vol 2. Scombrids of the world: an annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. FAO Fisheries Synopsis 125. Rome (Italy).

Eveson JP, Million J, Sardenne F, Le Croizier G (2015) Estimating growth of tropical tunas in the Indian Ocean using tag-recapture data and otolith-based age estimates. Fish Res 163:58–68.

Farley J, Clear N, Leroy B, et al (2003) Age and growth of bigeye tuna (*Thunnus obesus*) from the eastern and western AFZ. *CSIRO Marine Research Report to the Fisheries Research and Development Corporation. 2000/100* . Hobart, TAS: CSIRO.

Farley JH, Clear NP, Leroy B, et al (2006) Age, growth and preliminary estimates of maturity of bigeye tuna, *Thunnus obesus* , in the Australian region. Mar Freshw Res 57:713–724.

Farley JH, Williams AJ, Hoyle SD, et al (2013) Reproductive dynamics and potential annual fecundity of South Pacific albacore tuna (*Thunnus alalunga*). PLoS One 8:e60577.

Grande M, Murua H, Zudaire I, et al (2014) Reproductive timing and reproductive capacity of the Skipjack Tuna (*Katsuwonus pelamis*) in the western Indian Ocean. Fish Res 156:14–22.

Hunter J, Lo N, Leong R (1985) Batch fecundity in multiple spawning fishes. NOAA Tech Rep NMFS 36K1-F25:67–78.

Hunter J, Macewicz B (1985) Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish Bull 83:119–136.

IOTC (2015) Outcomes of the 17th session of the Scientific Committee.

Juan-Jordá MJ, Mosqueira I, Freire J, Dulvy NK (2013) Life in 3-D: life history strategies in tunas, mackerels and bonitos. Rev Fish Biol Fish 23:135–155.

Kume S, Joseph J (1966) Size composition, growth and sexual maturity of bigeye tuna, *Thunnus obesus* (Lowe), from the Japanese long-line fishery in the eastern Pacific Ocean. Inter-Am Trop Tuna Comm Bull 11:45–100.

Langley A, Herrera M, Sharma R (2013) Stock assessment of bigeye tuna in the Indian Ocean for 2012. IOTC-2013-WPTT15-30

Morgan M, Murua H, Kraus G, et al (2009) The evaluation of reference points and stock productivity in the context of alternative indices of stock reproductive potential. Can J Fish Aquat Sci 66:404–414.

Murua H, Motos L (2006) Reproductive strategy and spawning activity of the European hake *Merluccius merluccius* (L.) in the Bay of Biscay. J Fish Biol 69K1-F100:1288–1303.

Nootmorn P (2004) Reproductive biology of bigeye tuna in the eastern Indian Ocean. In: IOTC proceedings. In IOTC proceedings, pp 1–5

Pallares P, Pereira J, Miyabel N, Fonteneau A (1998) Atlantic bigeye tuna: overview of present knowledge (November 1996). INTER-Am Trop TUNA Comm Com Interam ATUN Trop 20.

Saborido-Rey F, Junquera S (1998) Histological assessment of variations in sexual maturity of cod (*Gadus morhua* L.) at the Flemish Cap (north-west Atlantic). ICES J Mar Sci J Cons 55:515–521.

Schaefer K (1998) Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Inter-Am Trop Tuna Comm Bull 21:201–272.

Schaefer K (2001) Reproductive biology of tunas. Fish Physiol 19 Block B Stevens E D 19:225–270.

Schaefer K, Fuller, DW, Miyabe, N (2005) Reproductive biology of bigeye tuna (*Thunnus obesus*) in the eastern and central Pacific Ocean. Inter-Am Trop Tuna Comm Bull 23:1–31.

Stéquert B, Marsac F (1989) Tropical tuna - surface fisheries in the Indian Ocean. FAO Fish. Tech. Pap. n^{o} 282. FAO, Rome

Stéquert B, Ramcharrun R (1996) La reproduction du listao (*Katsuwonus pelamis*) dans le bassin ouest de l'océan Indien. Aquat Living Resour 9:235–247.

Stobberup KA, Marsac F, Anganuzzi AA (1998) A review of the biology of bigeye tuna, *Thunnus obesus*, and the fisheries for this species in the Indian Ocean. In: Proceedings of the First World Meeting on Bigeye Tuna (Special Report No. 9). ICCAT, La Jolla, California. pp 81–128

Sun CL, Yeh SZ, Chang YJ, et al (2013) Reproductive biology of female bigeye tuna *Thunnus obesus* in the western Pacific Ocean. J Fish Biol 83:250–271.

Tsai W-P, Liu K-M, Punt AE, Sun C-L (2014) Assessing the potential biases of ignoring sexual dimorphism and mating mechanism in using a single-sex demographic model: the shortfin mako shark as a case study. ICES J Mar Sci J Cons fsu210.

Williams AJ, Farley JH, Hoyle SD, et al (2012) Spatial and sex-specific variation in growth of albacore tuna (*Thunnus alalunga*) across the South Pacific Ocean. PloS One 7:e39318.

Zhu G, Dai X, Song L, Xu L (2011) Size at sexual maturity of bigeye tuna *Thunnus obesus* (Perciformes: Scombridae) in the tropical waters: a comparative analysis.

Zhu G, Dai X, Xu L, Zhou Y (2010) Reproductive biology of bigeye tuna, *Thunnus obesus*,(Scombridae) in the eastern and central tropical Pacific Ocean. Environ Biol Fishes 88:253–260.

Zhu G, Xu L, Zhou Y, Dai X (2008) Length-frequency compositions and weightlength relations for bigeye tuna, yellowfin tuna, and albacore (Perciformes: Scombrinae) in the Atlantic, Indian, and eastern Pacific oceans. Acta Ichthyol Piscat 38:157–161.

Zudaire I, Murua H, Grande M, et al (2013a) Fecundity regulation strategy of the yellowfin tuna (*Thunnus albacares*) in the Western Indian Ocean. Fish Res 138:80–88.

Zudaire I, Murua H, Grande M, Bodin N (2013b) Reproductive potential of Yellowfin Tuna (*Thunnus albacares*) in the western Indian Ocean. Fish Bull 111:252–264.

Tables

Table 1. Summary of the sampled individuals by 5 cm L_F classes and by sex. Chi square test results are provided for size classes with more than 8 individuals.

class_fl	F	M	Chi-square	p-value
37.5	0	1	--	--
42.5	0	2	--	--
47.5	2	6	2	0.157
52.5	3	1	--	--
57.5	5	3	0.5	0.479
62.5	6	2	2	0.157
67.5	2	2	--	--
72.5	3	3	--	--
77.5	6	8	0.286	0.593
82.5	3	6	1	0.317
87.5	5	8	0.692	0.405
92.5	2	4	--	--
97.5	7	1	4.5	0.034*
102.5	2	0	--	--
107.5	0	3	--	--
112.5	5	4	0.111	0.739
117.5	3	3	--	--
122.5	7	3	1.6	0.206
127.5	7	7	0	1
132.5	11	5	2.25	0.134
137.5	15	19	0.471	0.493
142.5	19	20	0.026	0.873
147.5	33	35	0.059	0.808
152.5	24	25	0.020	0.886
157.5	16	23	1.256	0.262
162.5	10	14	0.667	0.414
167.5	0	6	--	--
172.5	1	1	--	--

Table 2. Summary of the number of individuals sampled by 5-cm L_F classes and maturity development for female bigeye tuna (BET).

	IP	DP			SCP				RsP	RgP
	PG	CA	Vtg1	Vtg2	Vtg3	GVM	GVBD	Hyd		
47.5	1	0	0	0	0	0	0	0	0	0
52.5	2	0	0	0	0	0	0	0	0	0
57.5	2	0	0	0	0	0	0	0	0	0
62.5	4	0	0	0	0	0	0	0	0	0
67.5	1	0	0	0	0	0	0	0	0	0
72.5	2	0	0	0	0	0	0	0	0	0
77.5	3	0	0	0	0	0	0	0	0	0
82.5	0	2	0	0	0	0	0	0	0	0
87.5	3	2	0	0	0	0	0	0	0	0
92.5	1	0	0	0	0	0	0	0	0	0
97.5	0	0	1	1	0	0	0	0	1	1
102.5	0	1	0	0	0	0	0	0	0	1
107.5	0	0	0	0	0	0	0	0	0	0
112.5	0	1	1	0	0	0	0	0	0	2
117.5	0	0	0	0	0	0	0	0	0	1
122.5	0	2	0	0	1	0	1	0	0	2
127.5	0	0	1	0	0	0	0	1	0	2
132.5	0	0	0	2	0	1	0	1	2	1
137.5	1	0	2	0	0	2	3	0	2	5
142.5	0	0	0	0	1	1	3	0	8	4
147.5	0	0	0	4	2	0	2	0	12	7
152.5	0	1	0	2	2	1	0	0	7	7
157.5	0	0	1	2	0	0	3	0	4	2
162.5	0	1	1	1	0	0	2	1	2	2
Total	20	10	7	12	6	5	14	3	38	37

Figures

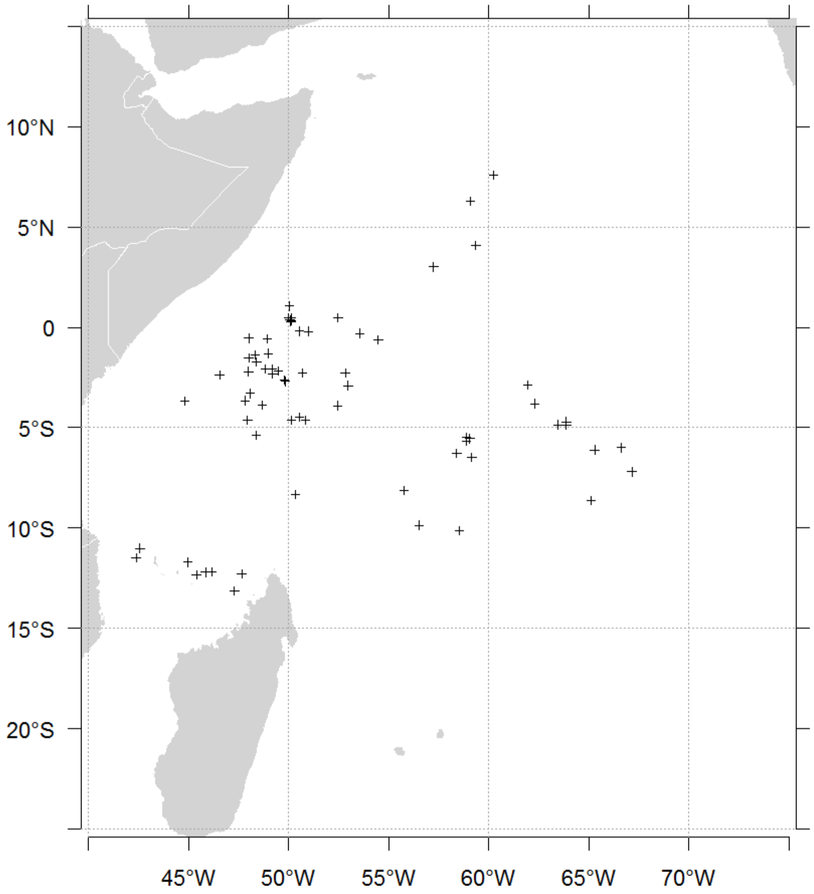

Figure 1. Fishing areas of the bigeye tuna (BET) caught by purse seiners in western Indian Ocean.

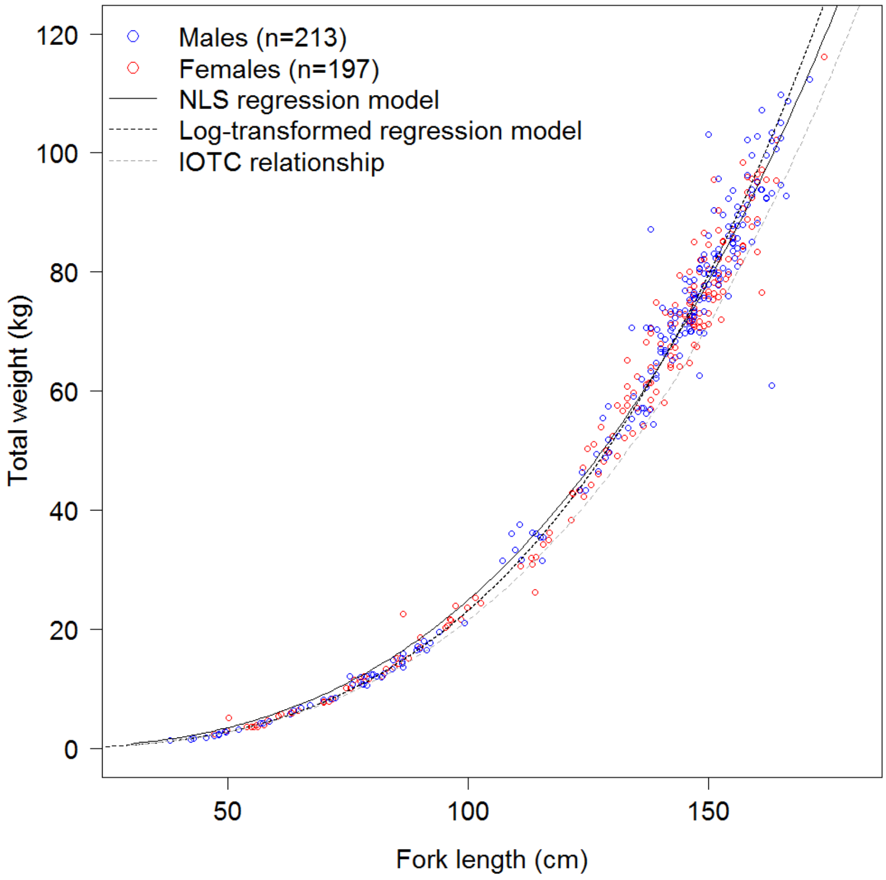

Figure 2. Relationship between fork length (L_F, cm) and body weight (W_T, kg) for male and female bigeye tuna (BET) sampled from 2010 to 2015.

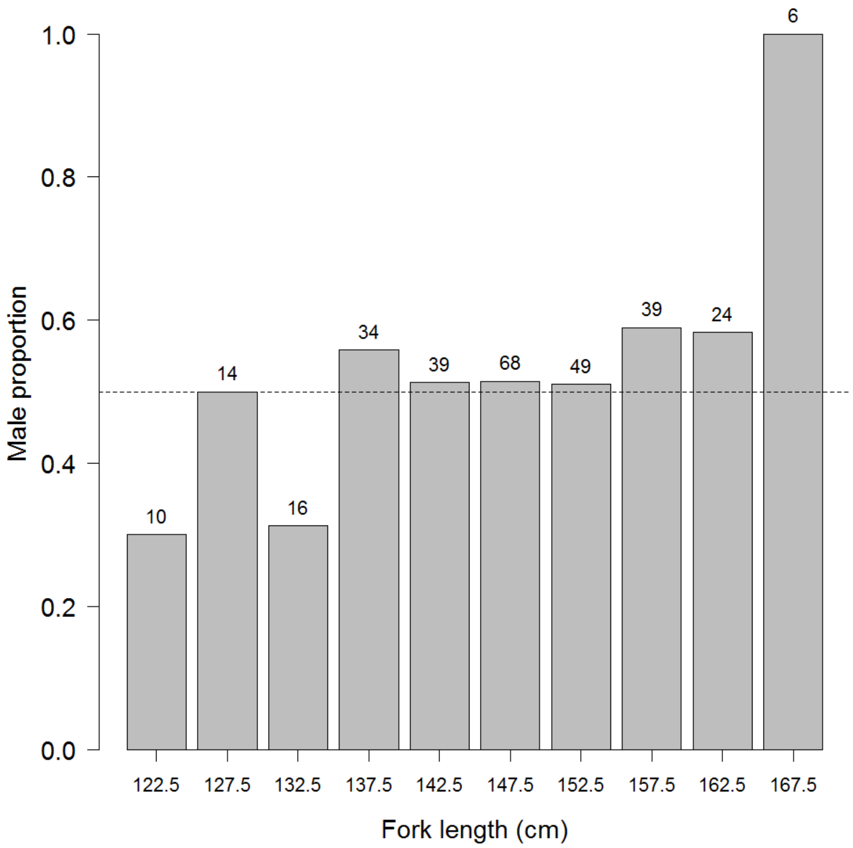

Figure 3. Sex-ratio variation by fork length of bigeye tuna (BET) in the western Indian Ocean.

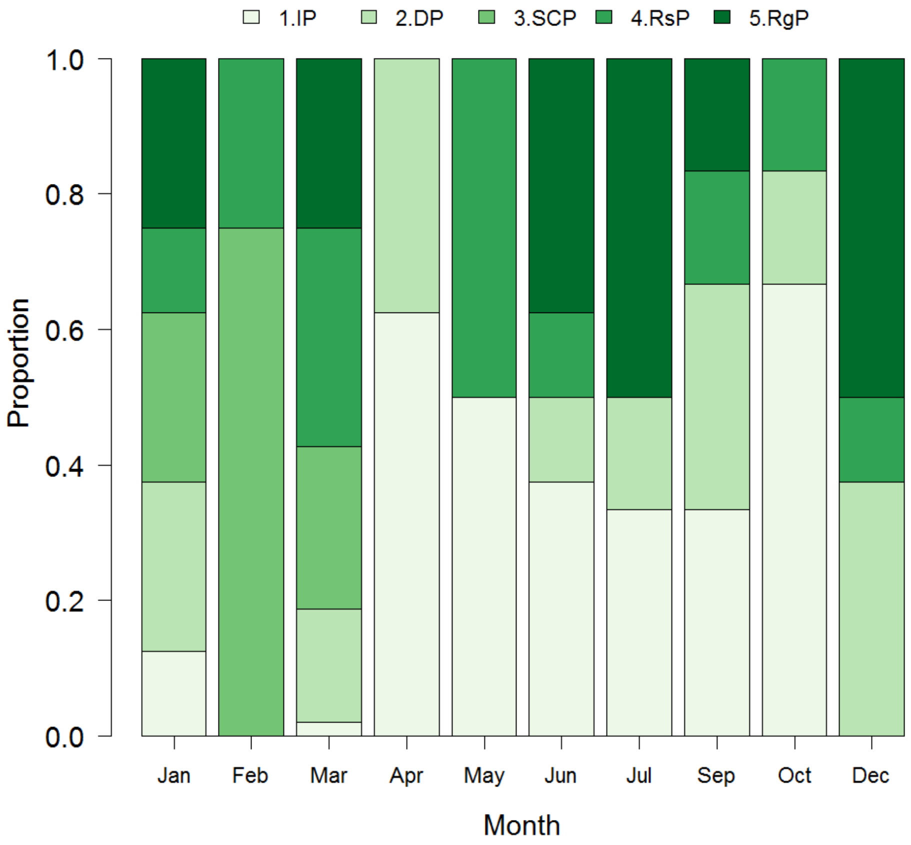

Figure 4. Monthly proportion of ovary development phases (1 = Immature phase; 2 = Developing phase; 3 = Spawning capable phase; 4 = Regressing phase; 5 = Regenerating phase) for female bigeye tuna (BET).

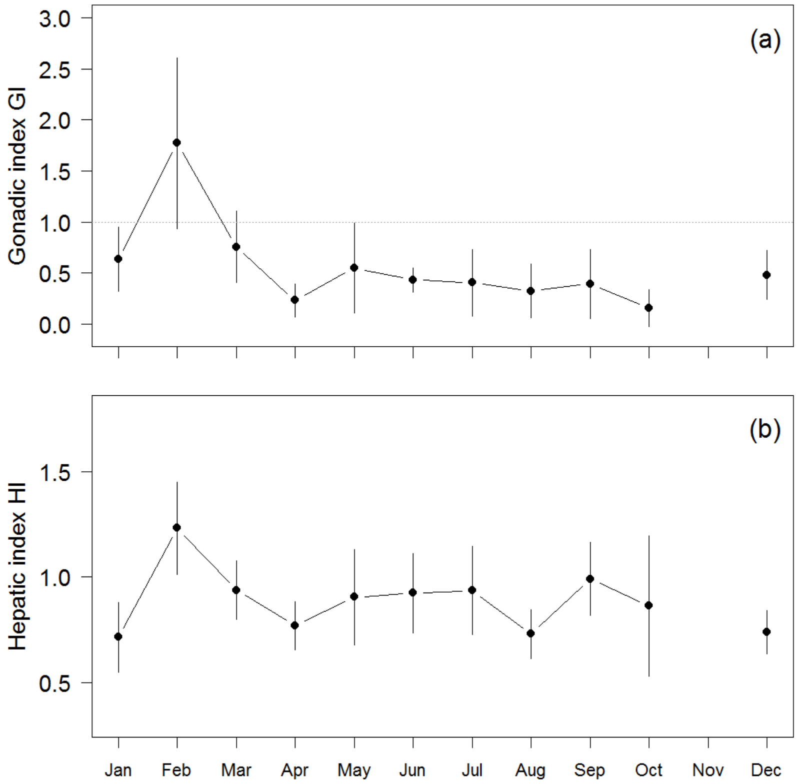

Figure 5. Seasonal variation of (a) gonado-somatic index *GSI* and (b) hepato-somatic index *HSI* for female bigeye tuna (BET) caught in the western Indian Ocean.

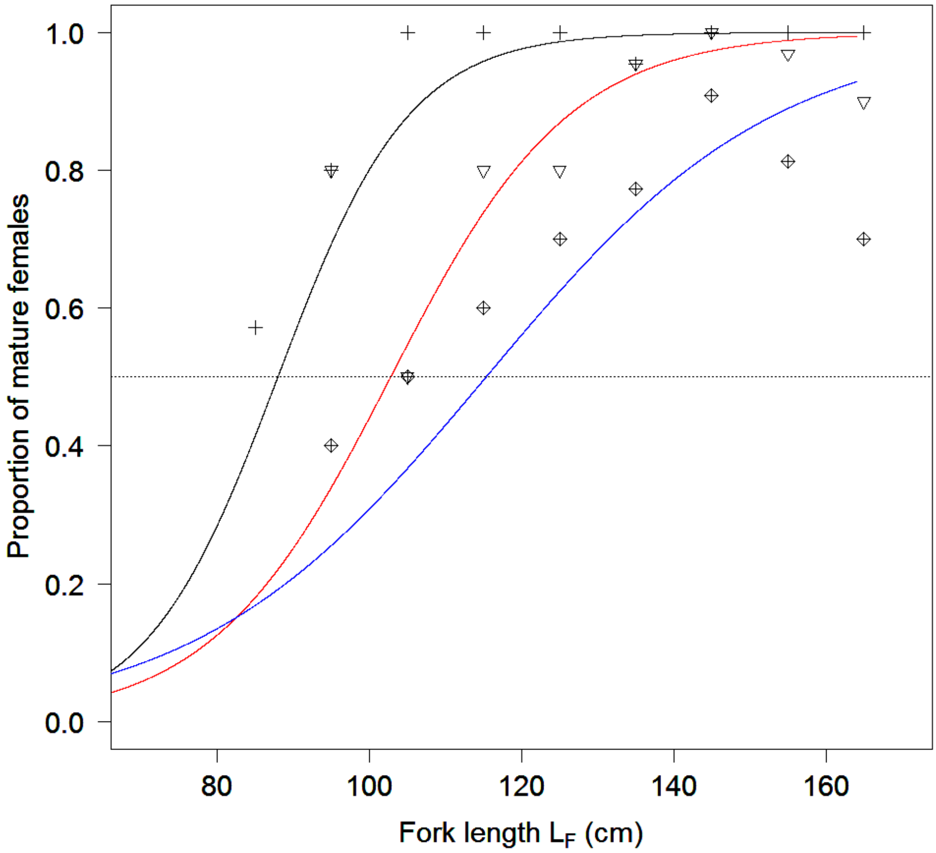

Figure 6. Proportion of mature female bigeye tuna (BET) in the western Indian Ocean at 10-cm L_F intervals. Crosses represent the proportions of females considered mature when their ovaries were at the cortical alveolar stage and onward; the black solid line indicates the logistic regression curve fitted to the data. Inversed triangles represent the proportions of females considered mature when their ovaries were at primary vitellogenic stage and onward; the red solid line indicates the logistic regression curve fitted to these data. Crossed squares represent the proportions of females considered mature when their ovaries were at tertiary vitellogenic stage and onward; the blue solid line indicates the logistic regression curve fitted to these data. The horizontal dotted line indicates L_{50}.

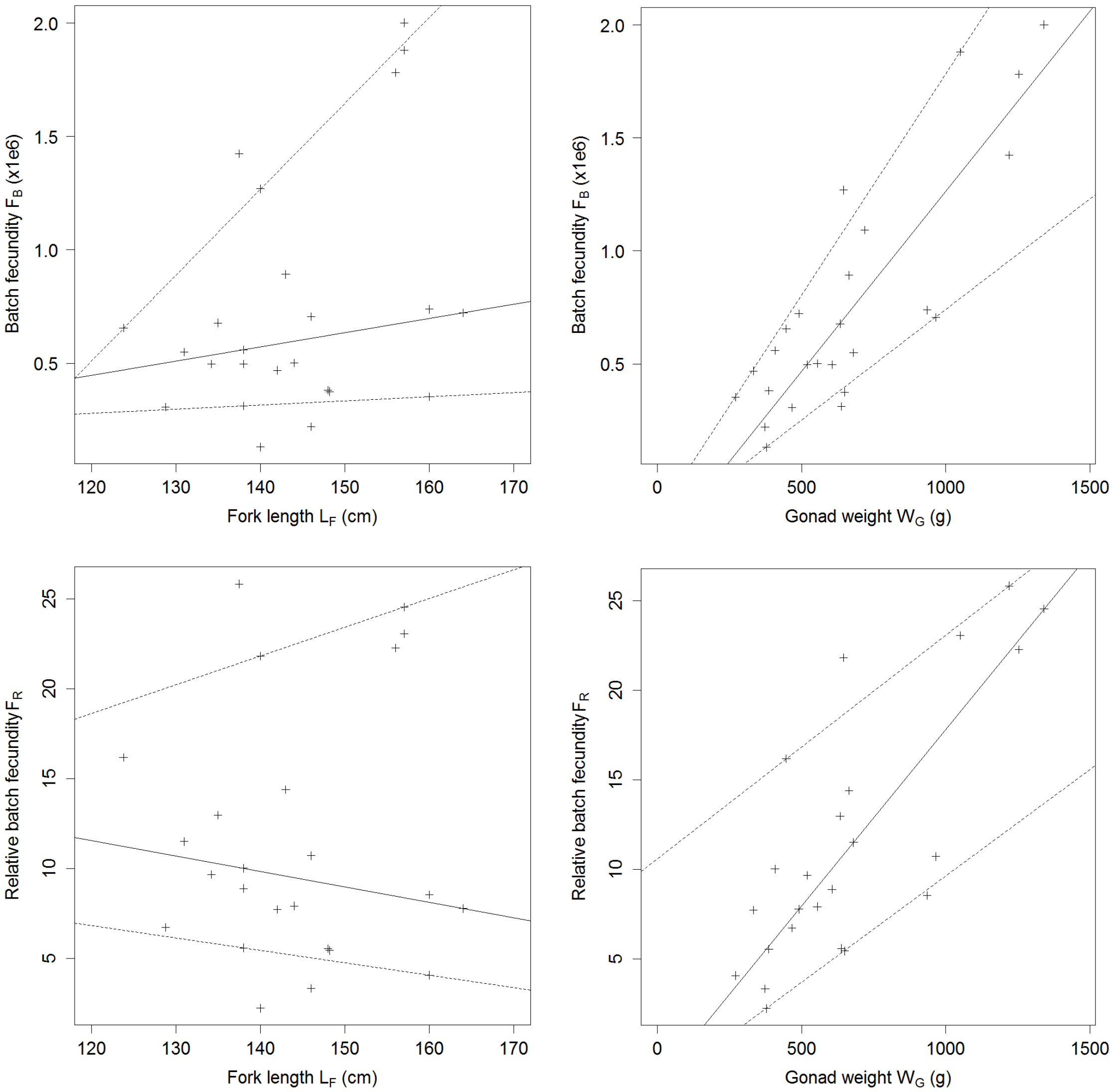

Figure 7. (Top from left to right) Relationship between batch fecundity (F_B) and fork length (L_F, cm) and F_B and gonad weight (W_G) for bigeye tuna from 2010 to 2015. (Bottom from left to right) Relationship between relative batch fecundity (F_{BR}) and fork length (L_F, cm) and F_{BR} and gonad weight (W_G) for bigeye tuna from 2010 to 2015.