

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

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4 ^{1,2}Zudaire I., ¹Chassot E., ²Murua H., ^{1,5}Dhurmeea Z., ⁴Cedras M., ¹Bodin N.

5 ¹IRD - research unit MARine Biodiversity, Exploitation & Conservation (MARBEC), Victoria, Mahé,
6 Seychelles

7 ²IKERBASQUE, Basque foundation for science, Bilbao, Spain.

8 ³AZTI-Tecnalia, Portu aldea s/n, Pasaia, Spain.

9 ⁴Seychelles Fishing Authority (SFA), Victoria, Mahé, Seychelles

10 ⁵Department of Biosciences, Faculty of Science, University of Mauritius, Réduit, Mauritius

11

12 Abstract

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

24

25 Keywords:

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

27

28 1. Introduction

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

44
45 Biological information on maturity, fecundity, and spawning season and location have been identified
46 by the Working Party on Tropical Tunas as high priority to the stock assessment (IOTC 2015).
47 Acquiring knowledge on these reproductive parameters improves the understanding of the fluctuations
48 in the population dynamic and hence, it allows to better assess population resilience to fishing and
49 environmental changes (Murua and Motos 2006; Morgan et al. 2009). However, information on BET
50 reproduction is still scarce (Juan-Jordá et al. 2013) and most of the efforts on this aspect have been
51 conducted in the Pacific Ocean (Farley et al. 2003; Schaefer et al. 2005; Farley et al. 2006; Zhu et al.
52 2010; Sun et al. 2013). In the Indian Ocean, the analysis of important reproductive traits has remained
53 preliminary and little information is available regarding sex-ratio, size at maturity and fecundity
54 (Stéquert and Marsac 1989; Stobberup et al. 1998; Nootmorn 2004; Ariz et al. 2006; Zhu et al. 2011).
55 Thus, the objective of this work is to contribute increasing knowledge on reproduction of BET by
56 providing reliable information on important reproductive traits (i.e., sex-ratio, size at maturity,
57 spawning period and fecundity) which are involved in the reproductive potential of this tuna species.

58

59 2. Material and methods

60 2.1. Field sampling

61 Bigeye tuna (n = 507; females = 204 and males = 216) was sampled from 2010 to 2015 in an
62 opportunistic sampling at processing factories of Seychelles and Mauritius. Individuals were caught by

63 purse-seine fleet operating in the Western IO (Figure 1). Fork length (L_F , cm), first dorsal length (L_{FD} ,
 64 cm), thorax length (L_T , cm) and total weight (W_T , Kg) were recorded from each fish. The gonads were
 65 then excised and the total weight (W_G , g) recorded. Gonadosomatic index (GSI) was calculated as
 66 $GSI = W_G / W_T \times 10^2$. A cross section of gonads of 4–5 cm was cut between the middle and end part of
 67 the right or left lobe and preserved in 4% buffered formaldehyde for reproductive analysis.
 68 Information regarding fishing date and area was obtained from vessels logbooks and plans of brine-
 69 freezing wells through close collaboration with the EU purse seine fleet and factories.

70

71 2.2.Length-weight relationship and sex-ratio

72 Multiple linear regression model was applied on the overall sampled BET (males and females) to
 73 assess the variability observed in weight as the function of length and sex. Sex ratio (SR) was
 74 calculated as the proportion of females by 5 cm L_F classes, and Chi square test was used to examine
 75 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
 76 and N_t is the total number of sampled fish.

77

78 2.3.Reproductive analysis

79 A 1-cm cross-section from the preserved portion of each ovary was embedded in paraffin, sectioned at
 80 5-7 μm and stained with Hematoxyline and Eosin. Ovaries were classified according to the most
 81 advanced oocyte stage present based on Zudaire et al. (2013a): (i) immature phase (P_I) which includes
 82 oocytes in the primary growth stage ; (ii) developing phase (P_D) which includes oocytes in the stages
 83 of cortical alveoli (CA) and primary (Vtg1) and secondary vitellogenesis (Vtg2); (iii) spawning-
 84 capable phase (P_{SC}) which includes oocytes in the stages of tertiary vitellogenesis (Vtg3), germinal
 85 vesicle migration (GVM), germinal vesicle breakdown (GVBD), and hydration (Hyd); (iv) regressing
 86 phase (P_{RG}); and (v) regenerating phase (P_R) characterized by the presence of maturity makers, late-
 87 stage atresia and a thicker ovarian wall than seen in immature fish. The atretic condition to appraise
 88 the P_{RG} was based on Hunter and Macewicz (1985) and the classification for atresia stages described
 89 in Zudaire et al. (2013a). However, the estimation of atresia for ovaries collected at the cannery entails
 90 difficulties due to their exposure to the brine conservation process used in PS. This conservation
 91 method produces breakages in the follicle wall and chorion and makes difficult the identification of
 92 different cytoplasm structures, hence, precise quantification of atresia was not always possible. No
 93 postovulatory follicles were found in the ovaries.

94

95 2.4.Size at maturity (L_{50})

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

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

105

106 2.5. Batch fecundity and relative batch fecundity

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

119

120 3. Results

121 3.1. Length-weight relationships and sex ratio

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

127

128 Sex ratio was analyzed by 5-cm size classes. A significant bias towards females was reported at small
 129 size classes (Table 1; L_F classes 95-100 cm). At intermediate and large size classes, no significant
 130 difference was found between sex although females were found to be more abundant at intermediate
 131 sizes (L_F 120-125 and 130-135 cm) while males started to become dominant at large sizes (Table 1; L_F
 132 > 150 cm) (Fig. 3).

133

134 3.2.Reproductive analysis and spawning season

135 According to the classification summarized in Table 2, 13.2% of females were at the P_I , 19.1% were at
 136 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
 137 females were mature when maturity threshold was set at CA oocyte development stage. Monthly
 138 assessment of the ovary development, described high spawning activity from January to March when
 139 ovaries were found more developed with high percentage of spawning females, especially in February
 140 with 75% of studied population at P_{SC} . In contrast, from April to October, no spawning activity was
 141 observed among females and most ovaries analyzed during this period were less developed, with high
 142 proportion of immature individuals (Fig 4). P_R and P_{RG} females were found all over the year showing
 143 high variability between months (from 12 to 50% and from 16 to 50% of the population, respectively).
 144 Highest values of P_{RG} individuals were found in May (50%), while for P_R the highest percentages
 145 (50%) were reported in August and December. The monthly mean GSI values also described a period
 146 of high reproductive activity from January (0.63 ± 0.32) to March (0.75 ± 0.35) with maximum values in
 147 February (1.77 ± 0.84) (Fig. 5). Afterwards, from April (0.23 ± 0.16) to December (0.48 ± 0.24), the GSI
 148 decreased and kept low.

149

150 3.3.Size at maturity

151 L_{50} was estimated at 88 ± 4 cm L_F when females with ovaries at CA stage and onward were considered
 152 mature. This estimation increased to 102 ± 4 cm L_F when Vtg1 was applied as maturity threshold and to
 153 115 ± 5 cm L_F when Vtg3 was applied (Fig 6).

154

155 3.4.Batch fecundity and relative batch fecundity

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

161

162 Spawning females were found only from January to March. Most of them were sampled in March, i.e.
 163 83% of the females. F_B was highly variable between months and no seasonal pattern was observed in
 164 spawning dynamics. The maximum mean F_B value was found in February (1.03 ± 0.54 million) and the
 165 minimum in January (0.4 ± 0.13 million). Analysis of variance (ANOVA) performed on F_B and F_{Brel} by
 166 month did not reveal any significant temporal differences at a 95% confidence level (ANOVA;
 167 $F_{(2,21)}=0.706$, $P=0.505$; $F_{(2,21)}=2.3$, $P=0.125$ respectively; Fig 7).

169

170 4. Discussion

171 4.1. Sex ratio

172 Although the small sample size for some of the size classes might weaken the overall interpretation of
173 the results, in the present study a significant difference on the sex ratio by length class was found at
174 small size BET, dominated by females as previously reported for eastern (Nootmorn 2004) and
175 southwestern IO (Ariz et al. 2006). However, at large sizes individuals ($L_F > 155$ cm), a higher
176 proportion of males was found among the studied population which is in accordance with previous
177 studies in the Indian (Nootmorn 2004), Pacific (Kume and Joseph 1966; Schaefer et al. 2005; Sun et
178 al. 2013) and Atlantic Ocean (Pallares et al. 1998). Two are more likely the explanations for the sex
179 ratio bias: (i) different sex-specific growth rate and (ii) different sex-specific natural mortality (Sun et
180 al. 2013). Kume and Joseph (1966) reported males' higher length frequency in Pacific Ocean and more
181 recently, further evidences of sexual dimorphism in tuna growth has been reported in *Thunnus*
182 *albacares* in the IO (Eveson et al. 2015) and *Thunnus alalunga* in Pacific Ocean (Williams et al.
183 2012), with males reaching larger sizes than females. Considering sexual dimorphism in population
184 dynamics might modify the outputs of stock assessment and eventually the stock status (Tsai et al.
185 2014). Data on sex ratio should be routinely collected for BET to complement our study and validate
186 the hypothesis of increasing proportion of males in the population at large sizes.

187

188 4.2. Reproductive analysis and spawning season

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

201

202 4.3. Size at maturity

203 In the current study, three different L_{50} estimates were provided derived from the three maturity
 204 thresholds applied on data (i.e., CA $L_{50} = 88 \pm 4$ cm L_F , Vtg1 $L_{50} = 102 \pm 4$ cm L_F and Vtg3 $L_{50} = 115 \pm 5$
 205 cm L_F). L_{50} has been widely reported in the Pacific Ocean, applying different maturity classification
 206 methods (i.e., macroscopic and histological analysis) and statistical models, which have led to a wide
 207 range of L_{50} values from 102 to 135 cm L_F (Schaefer et al. 2005; Farley et al. 2006; Zhu et al. 2011;
 208 Sun et al. 2013). The lack of a standardized methodology used in previous studies, however, makes
 209 difficult comparison of this important reproductive trait between regions and oceans (Sun et al. 2013).
 210 It is well recognized that histological identification of ovaries is the best method to accurately identify
 211 the oocyte development stages and hence to properly estimate size at maturity (Schaefer 2001). In the
 212 Indian Ocean, previous L_{50} estimations for BET were carried out by macroscopic identification of
 213 gonads reporting L_{50} at 88 cm L_F (Nootmorn 2004) and 119 cm L_F (Zhu et al. 2011). In the current
 214 study, applying histological analysis, L_{50} has been provided when maturity threshold is set at CA
 215 (Zudaire et al. 2013b; Grande et al. 2014). According to Brown-Peterson et al. (2011), an individual is
 216 considered mature when oocytes enter into CA stage. However, most of the previous tuna L_{50}
 217 estimations through histology have used vitellogenic stage of oocyte to fix maturity threshold
 218 (Schaefer et al. 2005; Sun et al. 2013). In the current work, both estimations applying Vtg1 and Vtg3
 219 ($L_{50} = 102$ cm L_F and $L_{50} = 115$ cm L_F , respectively) were into the ranged reported in the western
 220 Pacific Ocean (102 cm L_F ; Sun et al. 2013) and eastern and central Pacific Ocean (135 cm L_F ; Schaefer
 221 2005).

222

223 4.4. Batch fecundity and relative batch fecundity

224 To our knowledge, our analysis provides for the first time an estimation of F_B and F_{Brel} for BET in the
 225 western IO. The observed mean F_B (0.76 million oocytes) and F_{Brel} (11.54 oocytes per gram of body)
 226 are much lower than those reported in the eastern central Pacific (1.45 million oocytes and 24 oocytes
 227 per gram of body; Schaefer 2005) and western Pacific Ocean (3.06 million oocytes and 56.12 oocytes
 228 per gram of body; Sun et al. 2013). Besides a possible effect of the ocean-base variability, the fact that
 229 most of the analyzed individuals (83%) for fecundity were caught in March, close to the end of the
 230 reproductive season, is a factor that could underestimated our estimates of fecundity (Farley et al.
 231 2013). Thus, an increase of the sampling coverage, from December to March, is required for a
 232 comprehensive description of the spatiotemporal dynamic in reproductive potential of BET in the
 233 western IO.

234

235 In the current study, F_B and F_{Brel} were not related significantly to L_F and W_T , in contrast to previously
 236 reported in the Pacific Ocean (Schaefer et al. 2005; Sun et al. 2013). F_{Brel} appeared highly variable
 237 with L_F , and a negative relationship was predicted. This pattern may suggest lower reproductive

238 investment at large individuals, however, further analysis is required to better study size specific
239 fecundity in BET in the western IO.
240

241 Acknowledgements

242 We are grateful to all staff of «Mauritius cannery» for helpful assistance during sampling operations.
 243 The work was partially funded by IRD and the European Data Collection Framework (DCF, Reg
 244 199/2008 and 665/2008). IZ was funded through the Postdoctoral Program of the Basque Government.
 245 This work also benefited from the French ANR-funded project EMOTION (ANR JSV7 007 01).

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326 Tables

327 Table 1. Summary of the sampled individuals by 5 cm L_F classes and by sex. Chi square test results
 328 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	--	--

329

330

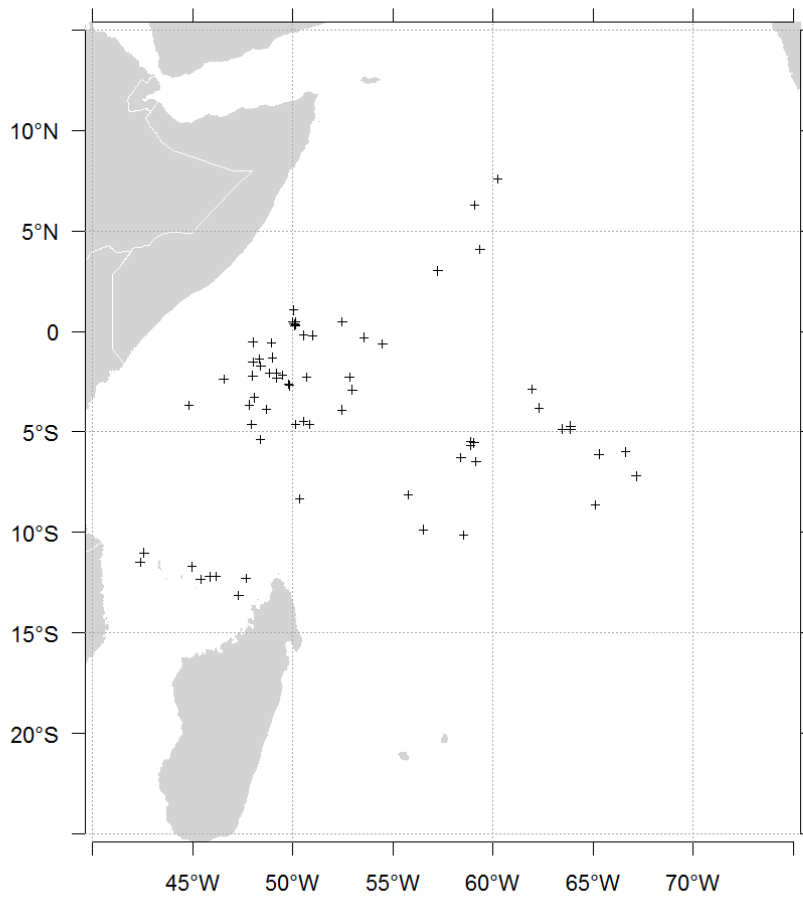
331 Table 2. Summary of the number of individuals sampled by 5-cm L_F classes and maturity development
 332 for female bigeye tuna (BET).

	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

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334

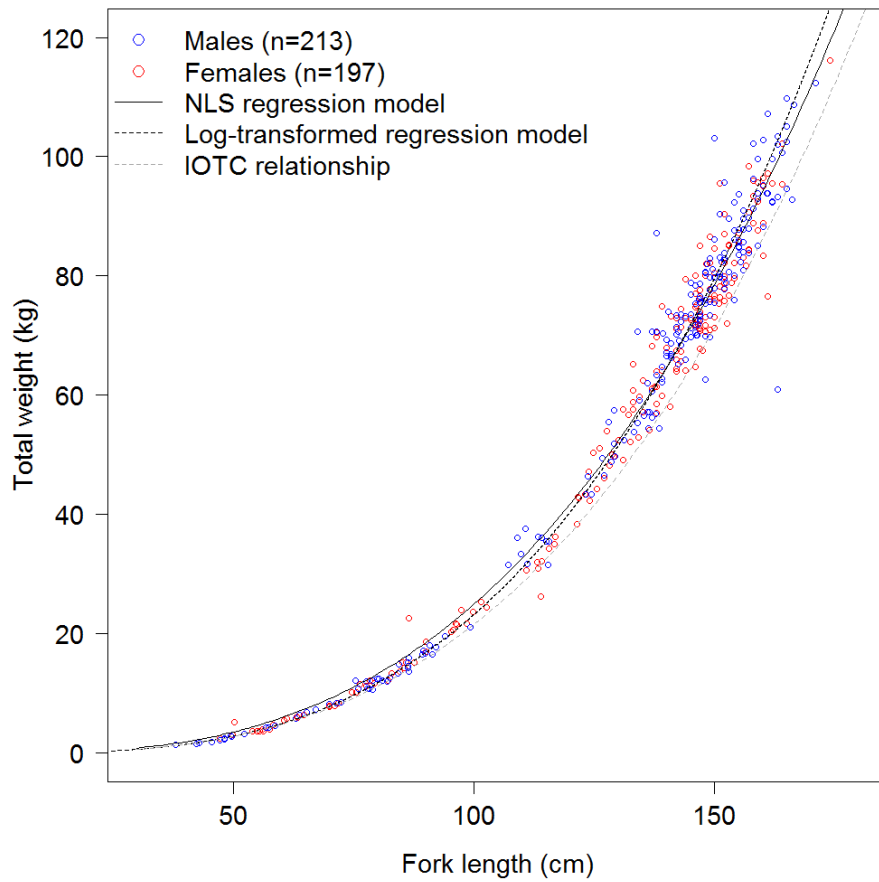
335 Figures



336

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

338

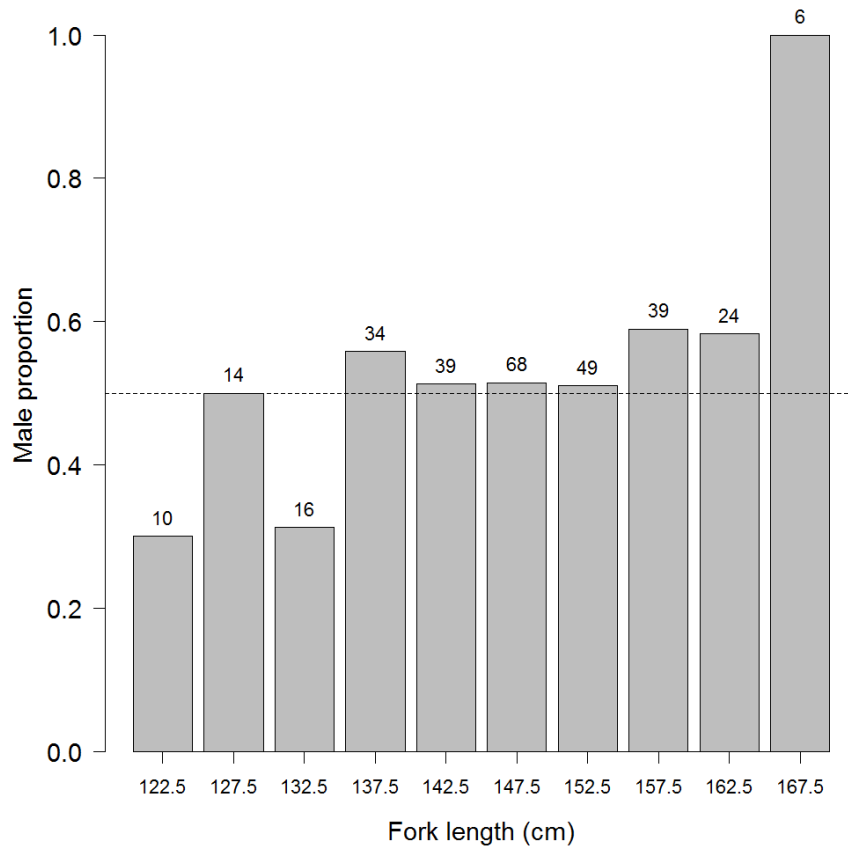


339

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

342

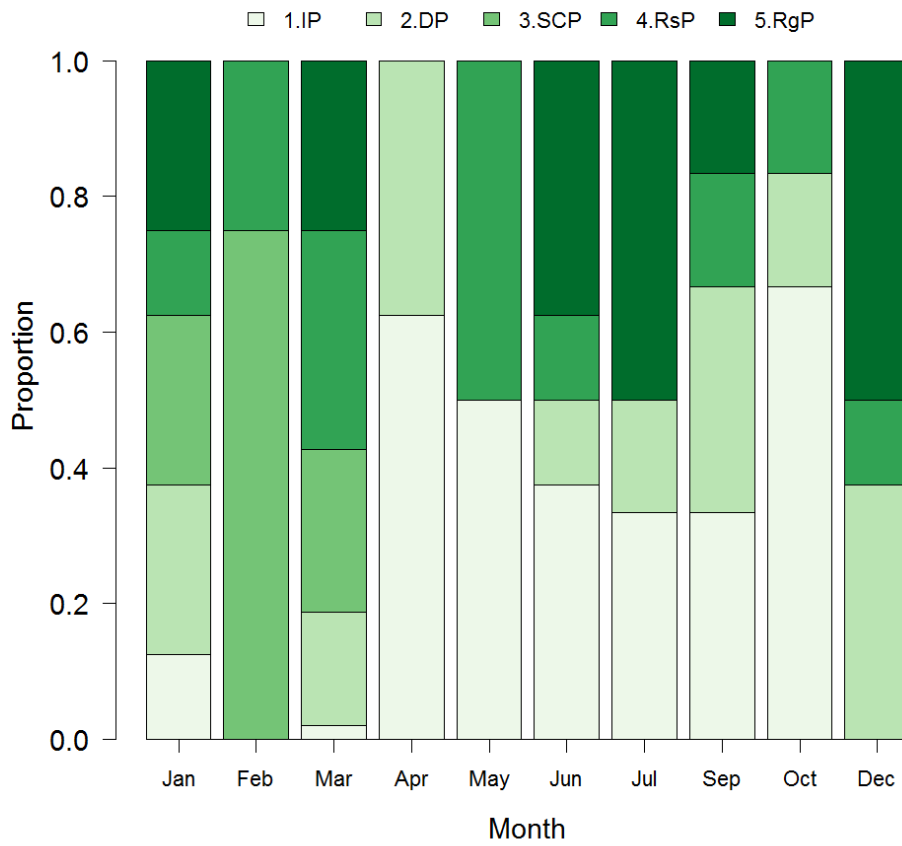
343



344

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

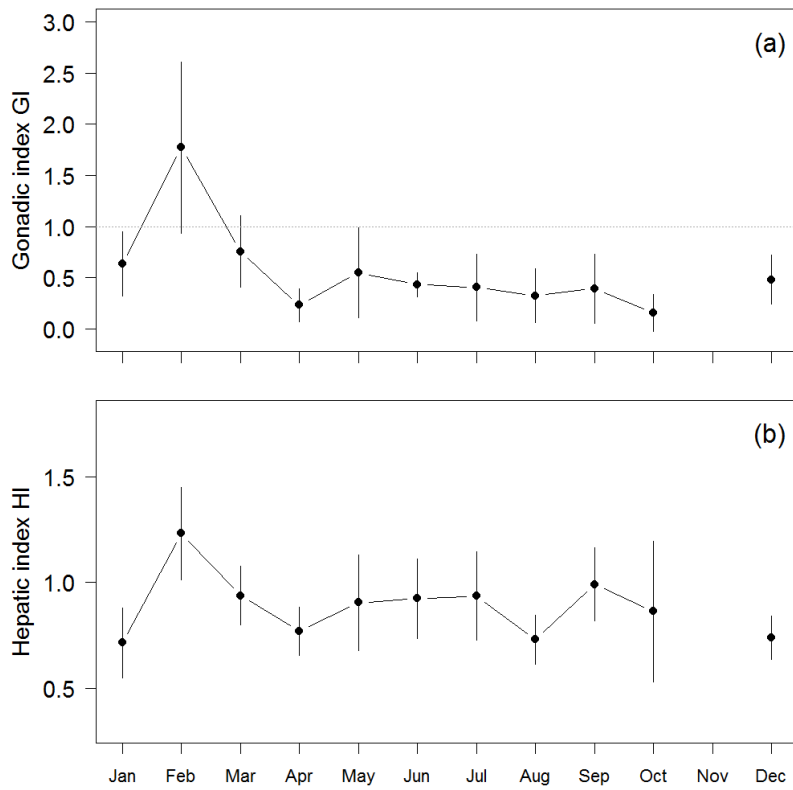
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347

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

351



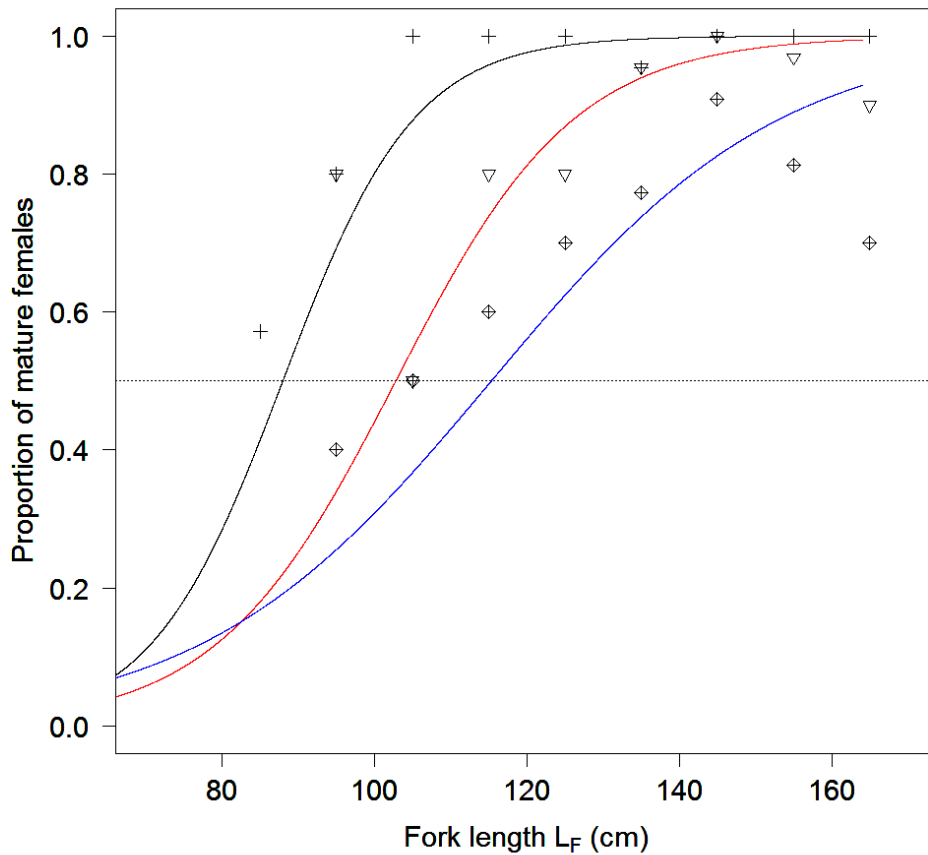
352

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

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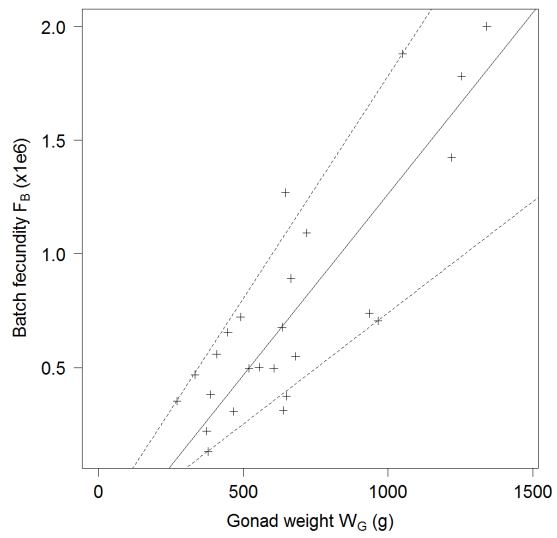
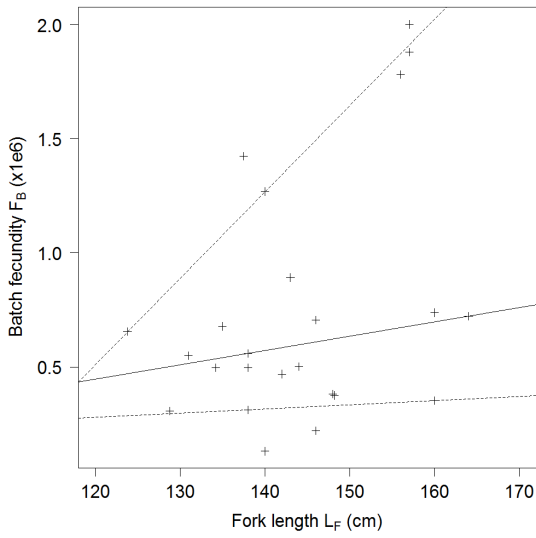
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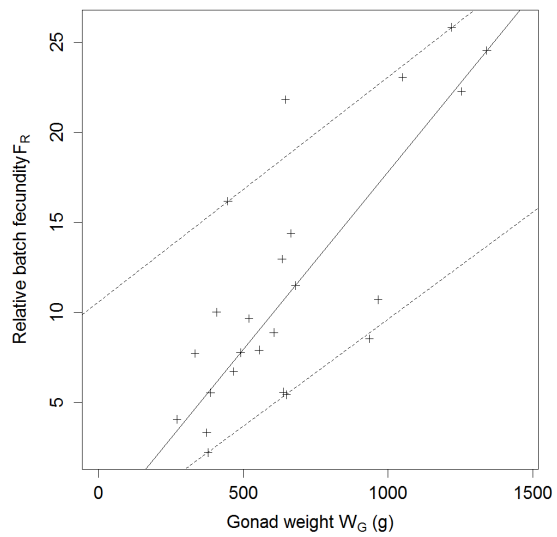
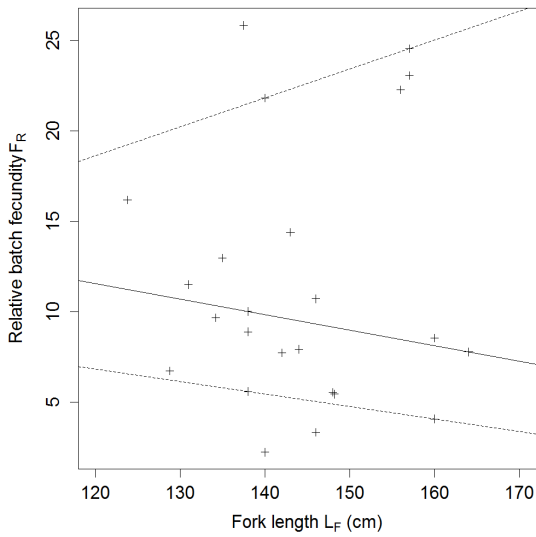
358

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

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370

371 Figure 7. (Top from left to right) Relationship between batch fecundity (F_B) and fork length (L_F , cm)

372 and F_B and gonad weight (W_G) for bigeye tuna from 2010 to 2015. (Bottom from left to right)

373 Relationship between relative batch fecundity (F_{BR}) and fork length (L_F , cm) and F_{BR} and gonad

374 weight (W_G) for bigeye tuna from 2010 to 2015.

375