Reproductive potential of Yellowfin Tuna (*Thunnus albacares*) in the western Indian Ocean

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Abstract—The reproductive biology of Yellowfin Tuna (*Thunnus albacares*) in the western Indian Ocean was investigated from samples collected in 2009 and 2010. In our study, 1012 female Yellowfin Tuna were sampled: 320 fish on board a purse seiner and 692 fish at a Seychelles cannery. We assessed the main biological parameters that describe reproductive potential: maturity, spawning seasonality, fish condition, and fecundity. The length at which 50% of the female Yellowfin Tuna population matures (L_{50}) was estimated at 75 cm in fork length (FL) when the maturity threshold was established at the cortical alveolar stage of oocyte development. To enable comparison with previous studies, L_{50} also was estimated with maturity set at the vitellogenic stage of oocyte development; this assessment resulted in a higher value of L_{50} at 102 cm FL. The main spawning season, during which asynchrony in reproductive timing among sizes was observed, was November–February and a second peak occurred in June. Smaller females (<100 cm FL) had shorter spawning periods (December to February) than those (November to February and June) of large individuals, and signs of skip-spawning periods were observed among small females. The Yellowfin Tuna followed a "capital-income" breeder strategy during ovarian development, by mobilizing accumulated energy while using incoming energy from feeding. The mean batch fecundity for females 79–147 cm FL was estimated at 3.1 million oocytes, and the mean relative batch fecundity was 74.4 oocytes per gram of gonad-free weight. Our results, obtained with techniques defined more precisely than techniques used in previous studies in this region, provide an improved understanding of the reproductive cycle of Yellowfin Tuna in the western Indian Ocean.

Manuscript submitted 7 September 2012.
Manuscript accepted 20 May 2013.
Fish. Bull. 111:252–264 (2013).
doi 10.7755/FB.111.3.4

Knowledge of reproductive traits is important for understanding population dynamics, including a population's resilience to fishing (Schaefer, 2001; Murua and Motos, 2006; Morgan et al., 2009). As alternatives to the traditional spawning stock biomass (SSB), reproductive potential indices have been proposed in which basic reproductive parameters are included as important factors that affect population productivity (Trippel, 1999; Morgan et al., 2009). These parameters include sex-ratio, the age and size of females, maturation ogive, fecundity, fish condition, and reproductive history. Inclusion of these biological parameters allows integration of fluctuations in a population's reproductive success into the assessment and management processes, in addition to estimation of spawning stock biomass (SSB) (Murua and Saborido-Rey, 2003; Murua et al., 2010). Hence, to improve the assessment and management of stocks, it is necessary to increase the quality and quantity of the basic reproductive data used to estimate these reproductive parameters (Korta, 2010).

Yellowfin Tuna (*Thunnus albacares*) is one of the major target species of the tuna fishery in the Indian Ocean. Total annual catch of Yellowfin Tuna in the Indian Ocean has increased significantly, since the early 1980s, with the advent of the purse-seine fishery. Average annual catch reached 473,896 metric tons (t) between 2003 and 2006 but decreased in 2007 and 2008 to around 320,000 t; in 2011, total annual catch was around 300,000 t (IOTC[1]).

The Yellowfin Tuna is a batch-spawner with asynchronous ovary organization (Schaefer, 2001) and indeterminate fecundity (Zudaire et al., 2013). This species can spawn with a frequency of around 1.5 days (McPherson, 1991; Schaefer, 2001) over a vast area of the tropical zone throughout the year (Itano[2]; Stéquert et al., 2001). Its spawning events, as with other tuna species, occur in rela-

[1] IOTC (Indian Ocean Tuna Commission). 2012. Report of the fifteenth session of the IOTC Scientific Committee. Victoria, Seychelles. IOTC Secretariat, P.O. Box 1011, Victoria, Seychelles.

tion to sea-surface temperature (>24°C), which seems to regulate spawning activity (Schaefer, 2001). In the Indian Ocean, spawning mainly occurs in the equatorial area (0–10°S) from December to March, and the main spawning grounds have been observed west of 75°E (IOTC[1]). However, other authors have reported variations in the spawning season of this species, describing periods between January and June (Zhu et al., 2008). Stéquert et al. (2001) related reproductive activity of Yellowfin Tuna with the north monsoon (main spawning period) from November to March and with the south monsoon (less reproductive activity) from June to August. Similarly, different estimates of maturity have been published for this species in several studies that used the same method to identify maturation stages. For example, the length at which 50% of females mature (L_{50}) was estimated at around 100 cm in fork length (FL) for Yellowfin Tuna in the Indian Ocean by the Indian Ocean Tuna Commission (IOTC[1]), at 108 cm FL in the western Pacific Ocean by McPherson (1991), at 92 cm FL in the eastern Pacific Ocean by Schaefer (1998), and at 104 cm FL for the equatorial western Pacific Ocean by Itano.[2]

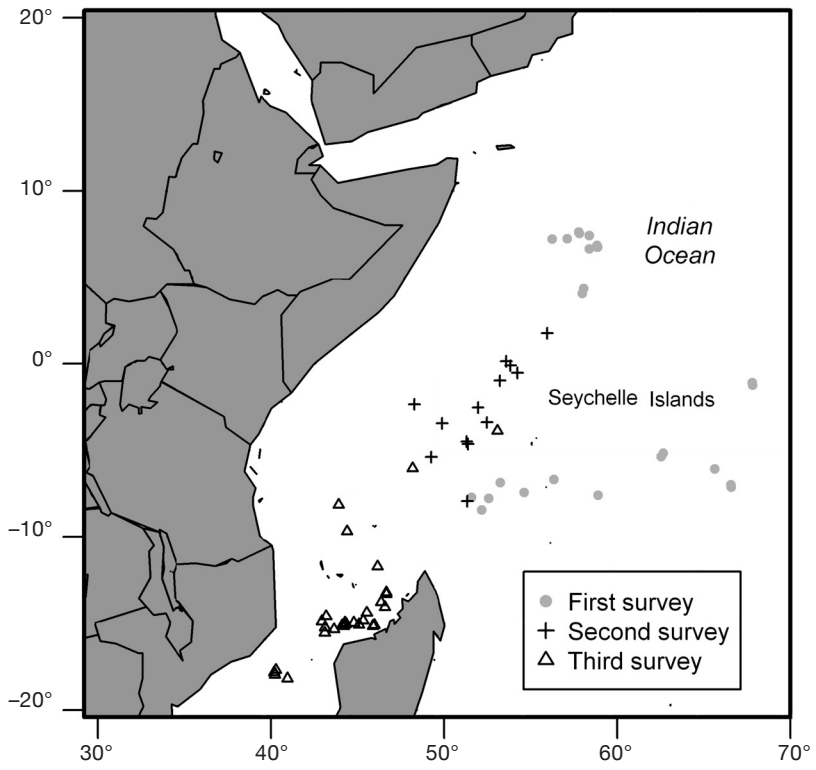

Figure 1

Map of locations where female Yellowfin Tuna (*Thunnus albacares*) were sampled in the first survey (22 January–23 March 2009), second survey (6 May–25 July 2009), and third survey (12 January–13 April 2010). The surveys were conducted aboard a commercial purse seiner in the western Indian Ocean to study the reproductive potential of Yellowfin Tuna in this region.

In spite of the ecological importance of Yellowfin Tuna and the significant decrease of its catches in various regions during recent years, there have been few studies that have focused on the reproductive biology of the Indian Ocean Yellowfin Tuna. This study aims to contribute to the knowledge of various reproductive traits essential for examination of the reproductive potential and population dynamics of Yellowfin Tuna in the western Indian Ocean, with an estimation of the following qualities: 1) length at 50% maturity; 2) spawning season; 3) fecundity; and 4) fish condition during reproduction.

Materials and methods

Field sampling

Sampling was done by scientific observers during 3 surveys conducted on board a commercial purse seiner in the western Indian Ocean during 2009 and 2010 (Fig. 1). At sea, during these surveys, 320 female Yellowfin Tuna were sampled. In addition, 692 ovaries from female Yellowfin Tuna that were captured by the purse-seine fleet that operated in the western Indian Ocean during the same period were collected at the Seychelles cannery (Table 1). Yellowfin Tuna were identified at sea and in the cannery through the use of characters given in Collette and Nauen (1983). Fork length (in centimeters), total weight (in kilograms), sex, maturation stage and gonad weight (in grams) were recorded for each individual. Liver weight (in grams) was measured only in females that were sampled at sea. Their ovaries were removed and weighed to the nearest gram. A cross section of the gonad of 4–5 cm was cut between the middle and end part of the right or left lobe and preserved in 4% buffered formaldehyde immediately after collection until it could be processed in the laboratory.

In the laboratory, cross sections (~1 cm) from the preserved portions of 819 ovaries were embedded in resin, sectioned at 3–5 µm, and stained with hematoxilyn and eosin (Korta, 2010). The histological classification of Yellowfin Tuna ovaries followed the criteria

[2] Itano, D. G. 2000. The reproductive biology of yellowfin tuna (*Thunnus albacares*) in Hawaiian waters and the western tropical Pacific Ocean: project summary. Pelagic Fisheries Research Program (PRFP), Joint Inst. Mar. Atmospheric Research (JIMAR), Univ. Hawaii (UH), HI. JIMAR contribution 00–328, p. 69. JIMAR, MSB 312, 1000 Pope Road, Honolulu, HI 96822.

Table 1

Period of sampling, ranges of fork lengths of tuna sampled, number of females sampled in each survey, and number of females used in different analyses for our study of the reproductive potential of Yellowfin Tuna (*Thunnus albacares*) in the western Indian Ocean. Analyses included the histological analysis of ovaries (Hist.), analysis of fecundity (Fec.), and analysis of the condition indices of gonadosomatic index (GSI), hepatosomatic index (HSI), and condition factor (*K*).

Survey	Sampling period	Length (cm)	Females sampled	Hist.	Fec.	GSI	HSI	*K*
1	22/01/2009–23/03/2009	37–158	114	110	6	106	105	106
2	5/06/2009–25/07/2009	30–161	95	95	5	95	77	95
3	03/04/2010–21/05/2010	31–157	114	114	–	95	94	95
Cannery	12/01/2010–13/04/2010	61–147	692	500	31	511	–	511

described in Zudaire et al. (2013). On the basis of terminology used in Brown-Petersen et al. (2011) and applied to Yellowfin Tuna (Zudaire et al., 2013), the ovaries were classified according to the most advanced oocyte stage present in the ovary: *immature phase* (including the primary growth stage [PG]), *developing phase* (including the cortical alveolar [CA], primary vitellogenesis [Vtg1], and secondary vitellogenesis [Vtg2] stages), *spawning-capable phase* (including the tertiary vitellogenesis [Vtg3], germinal vesicle migration [GVM], and hydration stages), and *regenerating phase*. The different stages of alpha-atresia were classified according to Zudaire et al. (2013). The ovaries collected at the cannery were not included in the analyses of atresia because they had been exposed to brine preservation used on board purse seiners, making it impossible to quantify alpha-atresia precisely. The ovaries collected at sea and at the cannery were analyzed for the identification of postovulatory follicles; however, no postovulatory follicles were found in these ovaries.

Length at 50% maturity

All females included in this analysis were staged histologically. L_{50} was calculated by fitting the proportion of mature females by 5-cm size classes to a logistic equation (Ashton, 1972; Saborido-Rey and Junquera, 1998):

$$P_{\text{mature}} = e^{\alpha+\beta L}/1+e^{\alpha+\beta L},$$

where P_{mature} = the predicted proportion of mature females;
L = the FL in centimeters; and
α and β are the coefficients of the logistic equation.

The L_{50} was estimated as the ratio of the coefficients ($-\alpha^*\beta^{-1}$). A nonlinear regression (the Marquardt method without restrictions; Marquardt, 1963) was used to fit the logistic equation to the data. The curve of L_{50} was estimated on the basis of the assumption that females with ovaries at the cortical alveolar stage onward were mature (Brown-Peterson et al., 2011). A second criterion was used to enable comparisons of our results with results reported in previous publications (Schaefer, 1998; Itano[2]; Zhu et al., 2008): females with cortical alveolar oocytes at the most advanced developmental stage were considered immature and females with advanced vitellogenic oocytes were considered mature.

Condition indices

Three condition indices were measured to estimate the condition of females: the gonadosomatic index (GSI), hepatosomatic index (HSI), and condition factor (*K*). These 3 indices were defined in this manner:

$$GSI = (W_g/W) \times 10^2;$$
$$HSI=(W_l/W) \times 10^2;$$
$$K=(W/L^3) \times 10^2;$$

where Wg = gonad weight;
W_l = liver weight;
W = fish gonad-free weight in grams; and
L = FL in centimeters.

The seasonal variations in those indices and their effect on the reproductive cycle were analyzed by month. To identify possible physiological changes during the ontogeny of Yellowfin Tuna, the seasonal development of the 3 condition indices was analyzed in 2 size groups: fish <100 cm FL and fish >100 cm FL—the L_{50}'s adopted by the Indian Ocean Tuna Commission [IOTC[1]]). Tuna sampled at the cannery were not included in the HSI analysis because the livers of these specimens were not weighed.

Fecundity estimation

Batch fecundity (BF), the total number of oocytes released per batch, was estimated for 40 ovaries with the gravimetric method (Hunter et al., 1989) by counting the oocytes in the germinal vesicle migration or hydration stages. Homogeneity in oocyte density among

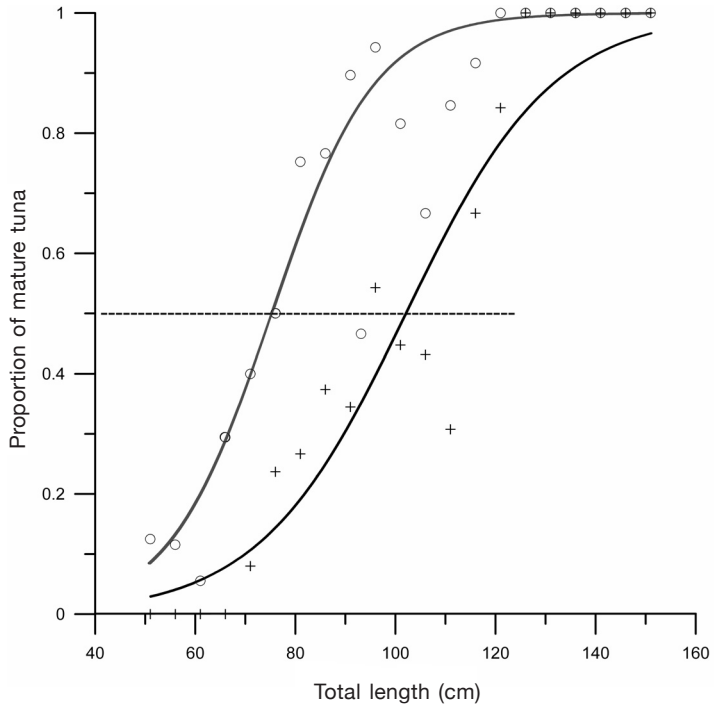

Figure 2

Proportion of mature female Yellowfin Tuna (*Thunnus albacares*) in the western Indian Ocean at 5-cm length intervals and fitted to a logistic regression curve in our study of the reproduction potential of this species in this region. Circles represent the proportions of females considered mature when their ovaries were at the cortical alveolar and later stages; the gray solid line indicates the logistic regression curve for these females. Crosses represent the proportions of females considered mature when their ovaries were at the vitellogenic and later stages; the dark solid line indicates the logistic regression curve for these females. The horizontal, dotted line indicates L_{50}, the length at which 50% of the female Yellowfin Tuna population were mature.

whole ovaries was assumed on the basis of previous studies on tuna (Stéquert and Ramcharrun, 1996). For BF analyses, 3 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, 1987, 1996, 1998). Batch fecundity was calculated as the weighted mean density of the 3 subsamples multiplied by the total weight of the ovary. A threshold of 10% for the coefficient of variance was applied for the 3 subsamples, and when this threshold was surpassed, more subsamples were counted to reach it. Relative batch fecundity (BFrel) was estimated by dividing the BF by the gonad-free weight of the fish. The relationships between the BF and BFrel with the FL, weight, and condition indices (GSI, HSI, and *K*) of females were determined. The seasonal trend in fecundity was analyzed through estimation of monthly mean BF and BFrel.

Statistical analyses

A nonparametric Kruskal-Wallis test (*H*-test) was applied to determine differences in the GSI, HSI, and *K* among months and between maturation stages. The relationships between the BF and BFrel and other biological parameters, such as length, weight, and condition indices (HSI and *K*), were analyzed through application of simple correlation and regressions. Analysis of variance (ANOVA) was applied to analyze the differences in the estimates of mean BF and mean BFrel by month during the spawning season.

Results

Length at 50% maturity

L_{50} was estimated to be 75 cm FL when females with ovaries at the CA stage and onward were considered mature. This estimate increased to 102 cm FL when the second criterion was applied (i.e., when the maturity threshold was defined as the presence of advanced vitellogenic oocytes, Fig. 2). In both cases, the proportion of mature females by length provided a good fit to the logistic model (coefficient of determination [r^2]=0.89 and r^2=0.91, respectively) (Table 2).

Reproductive cycle

The analysis of the female maturation process throughout the year showed that 30.1% of the individuals sampled were in the immature phase, 44.4% were in the developing phase, 20.3% were in the spawning-capable phase, and 5.12% were in the regenerating phase (Table 3). Overall, 69.8% of the sampled females were in the mature state, 92.6% of which were reproductively active.

The analysis of the maturation process was carried out for 2 size groups: individuals >100 cm FL and individuals <100 cm FL. The females >100 cm FL showed ovaries more developed and closer to spawning from November to February and in June than in other months (Fig. 3A). The period between November and January was especially important because more than 90% of the females sampled were in the spawning-capable phase. In contrast, during April and May, there was no spawning activity for this size group (fish >100 cm FL), with 40% and 30% of the ovaries in the regenerating phase in each month, respectively. The occurrence of immature phase ovaries increased to 50% and 38% in April and May.

Table 2

Summary of logit parameters of the female maturity (L_{50}=length at which 50% of the population is mature) curve for 2 criteria used in our study of Yellowfin Tuna (*Thunnus albacares*) reproduction in the western Indian Ocean. The symbols α and β represent the coefficients of the logistic equation, and r^2 is the coefficient of determination. In criterion 1, the L_{50} was calculated with the assumption that females with ovaries at the cortical alveolar stage onward were mature. The L_{50} in the criterion 2 was estimated with the assumption that females with cortical alveolar oocytes as the most advanced developmental stage were immature and those with advanced vitellogenic oocytes were mature.

	Criterion 1		Criterion 2	
Parameters	α	β	α	β
Estimate	–8.654	0.113	–6.965	0.068
Standard error	1.604	0.021	1.246	0.012
	Estimates		Estimates	
Number of females	423		423	
$L_{50}(-\alpha / \beta)$	74.7 cm		102.0 cm	
r^2	0.89		0.91	

The females <100 cm FL showed a considerable predominance of immature phase ovaries from April to November with levels of 50% or higher (Fig. 3B). These percentages of immature phase ovaries decreased below 30% during December, January, and February, and the percentage of ovaries in the spawning-capable phase increased to 4.4%, 5.3%, and 6.9%, respectively, for each month. It is noteworthy that ovaries in the regenerating phase appeared during the spawning season for females <100 cm FL, with values of 8.9% and 10.5% in December and January, but ovaries in this phase for larger Yellowfin Tuna (>100 cm FL) appeared in April and May.

Condition indices

The monthly variation in the GSI of the previously defined 2 size groups showed statistically significant differences between months for fish <100 cm FL (H_{669}=136.9, P<0.01) and fish >100 cm FL (H_{313}=206.4, P<0.01). Females >100 cm FL had a peak in mean GSI values that coincided with the highest proportion of females in the spawning-capable phase from November to January (GSI>2.0). Afterward, mean GSI values decreased sharply with a minimum value in April of 0.26 (standard deviation [SD] of 0.0). In June, the mean GSI increased again to 0.98 (SD 0.5) in a second spawning period but with lower reproductive activity compared with the main spawning period (Fig. 4A). In contrast, females <100 cm FL had almost constant mean GSI values except in December (0.44 [SD 0.2]), January (0.52 [SD 0.3]), and February (0.43 [SD 0.3]), when the GSI increased slightly during the main spawning period of large specimens of Yellowfin Tuna. There was no increase in the mean GSI in June for the smaller size group (Fig. 4B).

The monthly variation in HSI and K of both size groups showed statistically significant differences between months: HSI for fish <100 cm FL (H_{154}=29.1, P<0.01) and for fish >100 cm FL (H_{122}=26.3, P<0.01), and K for fish <100 cm FL (H_{669}=175.5, P<0.01) and for fish <100 cm FL (H_{313}=30.6, P<0.01). For females >100 cm FL, K values had a pattern that was opposite the one seen in the GSI. The K of large females was low from November (1.82 [SD 0.1]) to January (1.80 [SD 0.0]) and increased from February (1.82 [SD 0.0]) to July (1.89 [SD 0.2]) (Fig. 4A). Except for January, the mean HSI values showed a similar pattern to the one observed in the GSI. The HSI values of females >100 cm FL decreased from February (1.27 [SD 0.3]) to April (0.61 [SD 0.1]) and then increased slightly from May (0.70 [SD 0.1]) to July (0.72 [SD 0.2]) (Fig. 4A). The data series for the HSI was shorter than the data series for the other 2 condition indices because no liver samples were collected in the cannery.

Oocyte developmental stage and condition indices

There were significant differences in the GSI (H_{275}=162.1, P<0.01), HSI (H_{275}=49.9, P<0.01), and K (H_{275}=10.68, P<0.05) between ovarian developmental phases. The GSI showed lowest values at the primary growth stage (0.23 [SD 0.1]) and values increased throughout the vitellogenesis process (1.13 [SD 0.8]) until the maximum values at GVM (2.17 [SD 0.7]) and hydration (1.98 [SD 0.8]) stages were reached. Afterward, the GSI showed a sharp decrease in the regenerating phase (0.44 [SD 0.3]) (Fig. 5). The HSI showed a decreasing trend from immature phase ovaries (0.94 [SD 0.2]) to ovaries in vitellogenesis (0.77 [SD 0.2]), and then it followed the pattern shown by the GSI, increasing from vitellogenesis to hydration stages (1.33 [SD 0.3]). The HSI had its minimum value in the regenerating phase (0.66 [SD 0.1]). The K followed the opposite trend from that of the GSI and HSI; it decreased from the immature phase (1.94 [SD 0.2]) throughout the maturation process, obtaining minimum values at the hydration stage (1.77 [SD 0.0]). The K increased in the regenerating phase (1.85 [SD 0.1]).

Fecundity Estimation

The estimated mean BF was 3.07 million oocytes and varied from 0.32 million to 6.91 million oocytes. The estimated mean BFrel was 74.4 oocytes per gram of gonad-free weight and fluctuated between 9.2 and 180.8 oocytes per gram of gonad-free weight. Batch fecundity

Table 3

Summary of oocyte developmental stages and corresponding reproductive phases by 5-cm size class (fork lengths) in our study of Yellowfin Tuna (*Thunnus albacares*) reproduction in the western Indian Ocean. The numbers of individuals in our study that were at each developmental stage are shown in the columns organized by histological classification of the ovaries (Brown-Peterson et al. 2011; Zudaire et al., 2013): immature phase, including the primary growth stage (PG); developing phase, including the cortical alveolar (CA), primary vitellogenesis (Vtg1), and secondary vitellogenesis (Vtg2) stages; spawning-capable phase, including the tertiary vitellogenesis (Vtg3), germinal vesicle migration (GVM), and hydration stages (Hydr.); and regenerating phase.

		Mature phases and developmental stages							
		Developing to spawning-capable							
Length (cm)	Immature phase PG	CA	Vtg 1	Vtg 2	Vtg 3	GVM	Hydr.	Regenerating	Total
48–53	15	2							17
53–58	45	6							51
58–63	51	3							54
63–68	12	5							17
68–73	15	8	1	1					25
73–78	19	10	5	1	2			1	38
78–83	26	51	8	7	4	1		8	105
83–88	25	42	17	5	6	2		10	107
88–93	6	32	16		3			1	58
93–98	4	28	16	12	4	2		4	70
98–103	7	14	7	3	5	1		1	38
103–108	17	12	6	4	2			10	51
108–113	4	14	1		1			6	26
113–118	1	3	1	1	6				12
118–123		3			13	2		1	19
123–128				1	12	5	1		19
128–133			1	3	20	11	1		36
133–138			1	2	21	16	1		41
138–143		4	1	3	11	5	1		25
143–148		1		1	2	3	1		8
148–153			1				1		2
Total		238	82	44	112	48	6	42	819
	247	572							

was positively related to GSI, length, and weight; BFrel was related only to GSI; HSI and *K* showed no significant relationship with BF or BFrel (Table 4). The GSI showed the best correlation with BF and BFrel (coefficient of correlation [*r*]=0.87 and *r*=0.89, respectively). In contrast, low values for r^2 were found for length and weight (0.25). The intercept of the regression line between the BF and fish weight relationship was significantly different from 0.00 ($P<0.05$), a result that could indicate that the number of oocytes produced per gram of female is not linearly related to weight, and, therefore, larger females produce more oocytes per gram of gonad-free weight than do smaller females (Fig. 6). A decrease in mean BF values from November (3.79 million) to June (2.26 million) was observed. Nevertheless, the ANOVA of the BF estimates by month did not reveal statistically significant relationships between months at a 95% confidence level (ANOVA; $F_{(5,42)}=1.52$, $P=0.2081$). The BF appeared to be highly variable by month, making it difficult to identify a clear pattern for female fecundity.

Discussion

Length at 50% maturity

Analyses of L_{50} for female Yellowfin Tuna in the Indian Ocean in other studies resulted in different estimates (Table 5). To our knowledge, our study is only the second one where the L_{50} of Yellowfin Tuna in the Indian Ocean has been examined by histological method. Timochina and Romanov[3] previously used a histological

[3] Timochina O. I., and E. V. Romanov. 1991. Notes on reproductive biology of Yellowfin tuna in the western Indian Ocean. IPTP (Indo-Pacific Tuna Development and Management Program), Coll. Vol. Work. Doc. TWS/91/32, 60 p. P.O. Box 2004, Colombo, Sri Lanka.

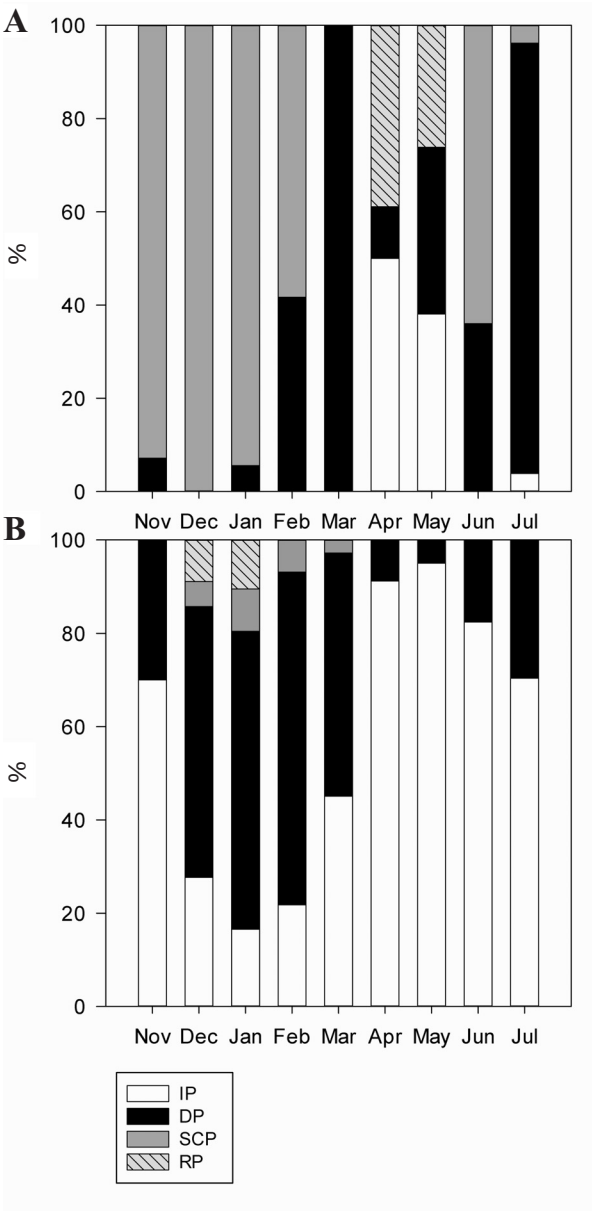

Figure 3

Proportion of female Yellowfin Tuna (*Thunnus albacares*) in different ovarian developmental phases by month and size: (**A**) >100 cm in fork length and (**B**) <100 cm in fork length. The phases of ovarian developmental shown in this graph are the immature phase (IP), developing phase (DP), spawning-capable phase (SCP), and regenerating phase (RP).

method to estimate the length at which all specimens achieve maturity. In our recent work, L_{50} was estimated at 75 cm FL when the maturity threshold was defined as ovaries in the CA stage. This length is significantly smaller than the L_{50} reported for all previous studies in the Indian Ocean (Table 5). In all of those studies, the L_{50} was estimated on the basis of macroscopic methods that defined the maturity threshold by the presence of advanced vitellogenic oocytes in the ovaries. Besides the natural variability in the length at maturity (Itano[2]), the main reasons for the difference in L_{50} between our study and previous studies are the use of different methods and oocyte stages to establish the maturity threshold for estimating L_{50}. Standardization of the selected maturity index and accurate estimation are required to enable direct comparisons between estimates and to avoid biases.

The cortical alveolar stage is the earliest sign of oocyte maturation (Brown-Peterson et al., 2011). Females in this developmental stage normally continue through vitellogenesis and spawn in the upcoming season (Wright, 2007). On the basis of the annual reproductive cycle and batch spawning behavior of Yellowfin Tuna, following the recommendation made by Lowerre-Barbieri et al. (2011), we suggest that Yellowfin Tuna females with ovaries in the cortical alveolar stage should be included in maturity estimates. Estimation of L_{50} through establishment of maturity in vitellogenic oocytes (Schaefer, 1998; Itano[2]; Zhu et al., 2008) has the disadvantage that L_{50} will be overestimated because maturing individuals (i.e., females with cortical alveolar stage oocytes) are categorized as immature (Lowerre-Barbieri et al., 2011). There is no information on how much individual growth occurs during the time lag between CA and vitellogenesis. Such information may improve estimation of L_{50} because growth between those stages may partly explain the difference in length at first maturity obtained with different oocyte maturation thresholds.

Reproductive cycle

On the basis of the histological evaluation of ovaries and the assessment of the seasonal variation in the GSI, 2 main reproductive periods were identified in our study. The first period identified occurred from November to February, and the second period occurred in June, with lower reproductive activity than the first period. Similar results were obtained by Stéquert et al. (2001), who related the spawning activity of Yellowfin Tuna with the monsoons. They identified that spawning activity was higher in the north monsoon (from November to March) than in the south monsoon (from June to August)—probably a result of the decrease in sea-surface temperature during the south monsoon period. Other authors identified only a single reproductive period: from January to June (Zhu et al., 2008), from January to March (Stéquert and Marsac, 1989), and from November to April (Nootmorn et al.[4]). The seasonal peaks in spawning described in this study were

[4] Nootmorn, P., A. Yakoh, and K. Kawises. 2005. Reproductive biology of yellowfin tuna in the eastern Indian Ocean. Indian Ocean Tuna Commission (IOTC),Working Party Tropical Tuna (WPTT), IOTC-WPTT-14, 378–385 p. IOTC Secretariat, P.O. Box 1011, Victoria, Seychelles.

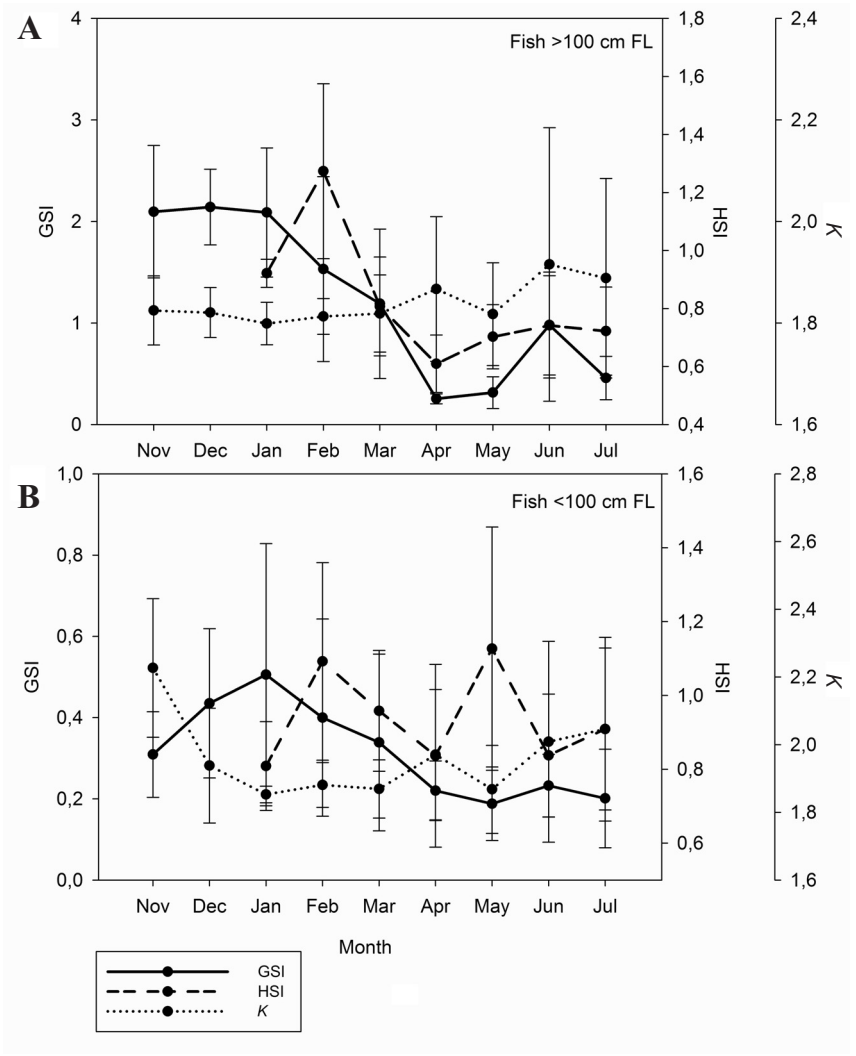

Figure 4

Mean monthly variation in the gonadosomatic index (GSI), hepatosomatic index (HSI), and condition factor (*K*) in our study of the reproductive potential of Yellowfin Tuna (*Thunnus albacares*) in the western Indian Ocean for females in two groups: (**A**) >100 cm in fork length (FL) and (**B**) <100 cm FL

supported by GSI values over 1.5, the value corresponding to that fish capable of reproducing (Nootmorn et al.[4]), observed from November to January. The GSI values for February and June below 1.5 could correspond to a period of lower spawning activity, in which the proportion of active females among the mature population decreased. The absence of samples from August to October affected the interpretation of the reproductive cycle (e.g., the commencement of the main spawning period).

The analysis of the reproductive cycle by size groups showed asynchrony in the reproductive activity between small and large Yellowfin Tuna. Larger and older individuals spawned earlier and longer in the season and had a higher activity than smaller individuals. This spawning behavior is in accordance with McPherson (1991) and Schaefer (1998), who described a positive relationship between the spawning fraction and female size. Our results showed asynchrony in the appearance of ovaries in the regenerating phase between small and large fish. Smaller individuals showed high percentages of ovaries in this phase earlier (December and January) than did large specimens (April and May). Ovaries of smaller individuals appeared in the regenerating phase within a period (from November to February) in which females generally exhibit high reproductive activity. This behavior can occur more often among young individuals maturing for the first time than among older fish (Murua et al., 2003), and it may be related to the energy balance between somatic growth and reproduction, an energy balance that is size related (Claramunt et al., 2007).

Another hypothesis that may explain the asynchrony in reproductive timing among sizes is that young females skip spawning events. The early appearance of ovaries in the regenerating phase occurred during the main peak of reproductive activity of mature individuals, and it is unlikely to be related to the end of the spawning season of young fish (Murua and Saborido-Rey, 2003). Female Yellowfin Tuna that skip spawning can be classified as *younger skipping* females (Secor, 2007). In these first-maturing females, maturation involves large physiological and behavioral transitions. They may not have the required energy resources and, therefore, forego reproduction. By skipping spawning, these females increase their growth rate and their chances of survival, resulting in increased lifetimes and reproductive outputs (Rideout and Tomkiewicz, 2011). However, the extended spawning season of Yellowfin Tuna, as well as the variable spawning period among individuals, complicates the identification of skipped spawning seasons in the reproductive cycle of females (Lowerre-Barbieri et al., 2009). Therefore, further research is needed to

Table 4

Coefficients of determination (r^2) and correlation (r) and P-values (P) for the relationship between batch fecundity (BF) and relative batch fecundity (BFrel) with different biological parameters: fork length, weight, gonadosomatic index (GSI), hepatosomatic index (HSI), and condition factor (K) in our study of Yellowfin Tuna (*Thunnus albacares*) reproduction in the western Indian Ocean.

	r^2	r	P
BF			
Length (cm)	0.2114	0.4598	<0.005
Weight (g)	0.2022	0.4497	<0.005
GSI	0.7579	0.8706	<0.001
HSI	0.0237	0.1541	0.6706
K	0.0611	–0.2472	0.1145
BFrel			
Length (cm)	0.0377	0.1943	0.2174
Weight (g)	0.0263	0.1622	0.3046
GSI	0.8099	0.8999	<0.001
HSI	0.0696	0.2639	0.4612
K	0.0184	–0.1357	0.3914

determine whether the appearance of regenerating phase ovaries among young individuals indicates that females have skipped the spawning season.

Condition indices related to reproduction

Condition indices are important parameters for tuning the estimation of reproductive potential (Marshall et al., 1999). Analysis with such indices throughout the spawning season allows the determination of energy allocation during reproduction (Murua and Motos, 2006). In our study, during the peak spawning period (November–February), GSI, HSI, and K reflected a seasonal pattern in the accumulation and depletion cycles of energy reserves. The increase in the GSI and HSI at the expense of K was observed both in smaller (<100 cm FL) and larger (>100 cm FL) females, and the exchange of energy was more pronounced in the larger size group. These 3 condition indices from March to July showed higher variability than in the first spawning period (from November to February), and no distinct pattern was evident. For the period of higher spawning activity (November–February), condition indices showed a clear pattern of energy mobilization from the muscle to the liver or gonad for reproduction. In contrast, during the second spawning period (June), energy was mobilized at a lower level because of lower spawning activity.

The protracted spawning season and population asynchrony in spawning activity of Yellowfin Tuna could mask temporal variations in energy allocation and the mobilization of the factors that were analyzed (Domínguez-Petit et al., 2010). Therefore, the assessment of variation in energy reserves by maturation phases was performed to study the energy cycle in females undergoing ovarian development (Alonso-Fernández and Saborido-Rey, 2012). The results showed a high energy investment in reproduction. The GSI showed an increase in the ovary mass from the immature phase to hydration stage, and the HSI described an increase of liver mass mainly between the vitellogenic process and maturation. This HSI pattern is evidence of the importance of the liver in the energy accumulation and synthesis of those energetic compounds (e.g., lipids and vitellogenin) essential for ovarian development (Domínguez-Petit et al., 2010). The decrease of K during the vitellogenic process and the low values of K at the GVM and hydration stages could indicate the role of the muscle in the mobilization of energy to the gonad or liver to fulfill the energetic requirements of maturation, principally during vitellogenesis (Zaboukas et al., 2006; Domínguez-Petit et al., 2010).

Table 5

Estimates of the length at 50% maturity (L_{50}) and the fork length at which all specimens achieve maturity (L_{100}) for female Yellowfin Tuna (*Thunnus albacares*) reported for previous studies in different areas of the Indian Ocean. The methods applied for the classification of ovaries were macroscopic (Macro.) and microscopic (i.e., histological, Micro.). The criterion for the maturity threshold in all of these studies was the presence of vitellogenic stage oocytes.

Studies	Estimation type	Method	Length (cm)
Stéquert and Marsac, 1989	L_{50}	Macro.	120–140
Hassani and Stéquert (*see fn. 5 in the text*)	L_{50}	Macro.	110–115
Nootmorn et al. (*see fn. 4 in the text*)	L_{50}	Macro.	110
Karpinski and Hallier[7]	L_{50}	Macro.	104–112
Zhu et al. 2008	L_{50}	Macro.	114
Timochina and Romanov (*see fn. 3 in the text*)	L_{100}	Micro.	120
Maldeniya and Joseph[8]	L_{50}	Macro.	100

[7] Karpinski, B., and J. P. Hallier. 1988. Preliminary results on yellowfin spawning in the western Indian Ocean. Indo-Pacific Tuna Development and Management Program (IPTP) Coll. Vol. Work. Doc.TWS/88/31, 50–59 p.

[8] Maldeniya, R., and L. Joseph. 1986. On the distribution and biology of yellowfin tuna (*T. albacares)* from the western and southern coastal waters of Sri Lanka. FAO/IPTP Coll. Vol. Work. Doc. 2: TWS/86/18, 21–32 p.

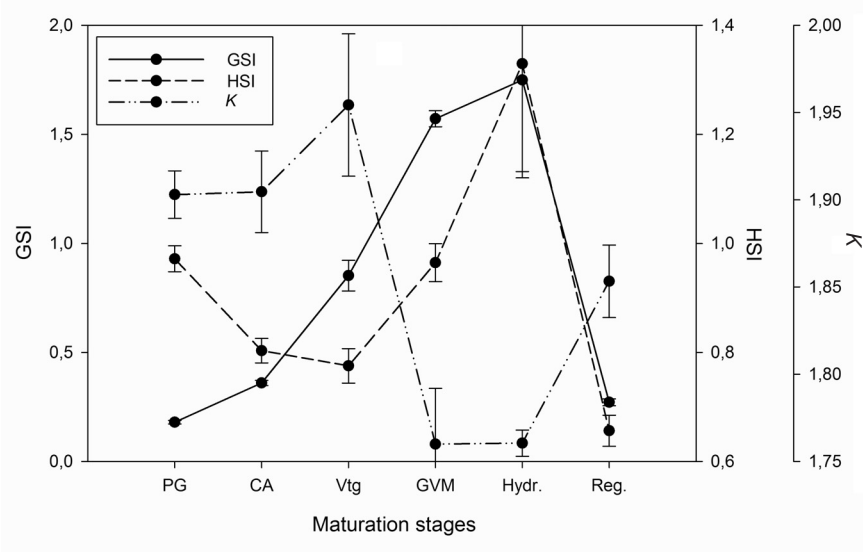

Figure 5

Mean variation in gonadosomatic index (GSI), hepatosomatic index (HSI), and condition factor (*K*) for Yellowfin Tuna (*Thunnus albacares*), in our study of the reproductive potential of this species in the western Indian Ocean, by oocyte developmental stage: primary growth (PG), cortical alveolar (CA), primary, secondary, and tertiary vitellogenesis (Vtg); germinal vesicle migration (GVM); hydration (Hydr.), and regenerating (Reg) stage.

The energy allocation strategy varies among organisms as an adaptive measure to deal with the fluctuations in the availability of energy in marine environments (Alonso-Fernández and Saborido-Rey, 2012). Subtropical and tropical waters with relatively low fluctuations in environmental conditions (e.g., in food supply, temperature, and photoperiod) are conducive habitats for species to offset the cost of the reproductive process by concurrent energy from feeding, without having to rely entirely on stored energy reserves (Alonso-Fernández and Saborido-Rey, 2012). Yellowfin Tuna continue to feed while they reproduce, and it has been suggested that the high spawning activity of this species depends on prey availability during spawning (Itano[2]). On the basis of our results, we suggest that Yellowfin Tuna, like other tropical species (Arrington et al., 2006), requires energy from feeding as well as from stored energy to carry out ovarian development. Therefore, Yellowfin Tuna could be described as a capital-income breeder (Alonso-Fernández and Saborido-Rey, 2012), in which the energy stored before reproduction is not enough to offset the cost of reproduction, and energy allocation from feeding is necessary for successful reproduction (Henderson and Morgan, 2002).

Fecundity estimation

Few studies have dealt with the fecundity of Yellowfin Tuna in the Indian Ocean. In our study, the estimated mean BF (3.1 million oocytes) is within the range reported by Hassani and Stéquert,[5] and in Table 6 by Timochina and Romanov[2] for the western Indian Ocean and by Sun et al.[6] for the western Pacific Ocean. However, our estimate is larger than the values reported by Schaefer (1996, 1998) for the eastern Pacific Ocean and by Itano[2] for the western Pacific Ocean. It is lower than the values reported by Itano[2] for the Hawaii area. Furthermore, the mean BFrel value (74.4 oocytes per gram of gonad-free weight) determined in our study for Yellowfin Tuna is slightly higher than the values described by Schaefer (1996, 1998) and Sun et al.[6] (Table 6), and it is considerably higher than the values reported by Itano[2]. Besides the geographic differences among studies, intrapopulation variability in fecundity (Schaefer, 1996) could be the main factor that caused the difference between the results of our study and previously published results.

The BF increased with female size and weight ($P<0.05$); however, the BF-length and BF-weight relationships showed low r^2 (<0.25) with high variability—a finding that could result from the asynchrony of the population spawning (i.e., with some individuals at the beginning and others at the end of their individual spawning season). The intercept of the regression line between the BF and weight was statistically different from zero, indicating that larger females spawn more oocytes per gram than smaller females; this dynamic in turn would contribute to increasing the egg production for large females (Domínguez-Petit and Saborido-Rey, 2010). However, the BF of fish of the same size varied greatly, indicating that other factors, such as fish condition during spawning, could also drive female productivity (Hassani and Stéquert[5]; Murua and Motos, 2006).

Experiments with captive Yellowfin Tuna showed evidence of a positive relationship between the daily food ratio and egg batch production (Margulies et al.,

[5] Hassani S., and B. Stéquert. 1990. Sexual maturity, spawning and fecundity of the yellowfin tuna (*Thunnus albacares*) of the Western Indian Ocean. Coll. Vol. IPTP (Indo-Pacific Tuna Development and Management Program) Doc. Vol. 4, p. 91–107. IPTP, P.O. Box 2004, Colombo, Sri Lanka.

[6] Sun, C., W. Wang, and S. Yeh. 2005. Reproductive biology of yellowfin tuna in the central and western Pacific Ocean. Western and Central Pacific Fisheries Commission (WCPFC). WCPFC-SC1, BI WP-1, 1–14 p.

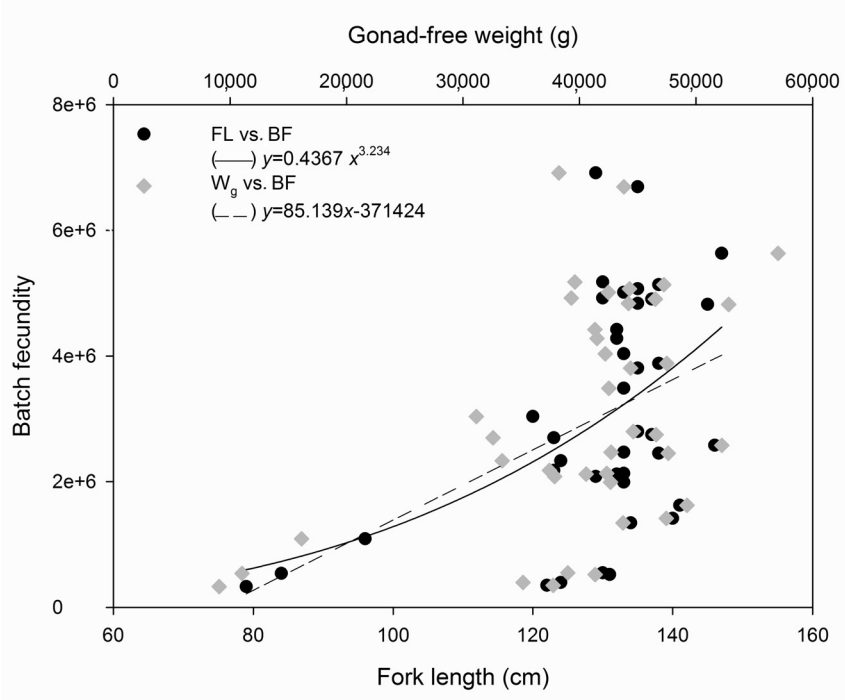

Figure 6

Linear regression between batch fecundity (BF) and fish gonad-free weight (W_g), and power function between BF and fork length (FL) for Yellowfin Tuna (*Thunnus albacares*) sampled in the western Indian Ocean in 2009 and 2010

2007). Lauth and Olson (1996) suggested that tuna may boost batch fecundity in response to greater amounts of forage, in accordance with the results reported by Itano[2] for the Pacific Yellowfin Tuna. Batch fecundity enhancement by feeding might explain the observed high interindividual variation in the BF. Apart from prey availability, other biotic and abiotic parameters, such as fish condition, genetic variation, geographic differences in sampling locations, and temperature, have been reported to be associated with variability in the productivity of fish species (Schaeffer, 1998; Murua and Motos, 2006).

Conclusions

Advances in the management of fish stocks rely to a great extent on updated knowledge of reproductive dynamics and its implementation in stock assessments. The results described here will contribute to the improvement of the understanding of the reproductive dynamics of Indian Ocean Yellowfin Tuna. The L_{50} was estimated at 75 cm FL with the maturity threshold set at the CA stage of ovarian development. Two reproductive periods were detected in which reproductive activity was higher in large females than in small ones. Similarly, large females had higher contribution of fecundity than did small females; however, more research on fecundity is required to investigate the principal factors that affect its variability at individual and population levels. We suggest that Yellowfin Tuna follow a capital-income breeder strategy during ovarian development, by mobilizing accumulated energy and incorporating energy from feeding. However, further research on the proximate composition (e.g., lipids and proteins) of this species through analyses of different tissues is required to obtain more precise descriptions of energy allocation and mobilization during the reproductive cycle of Yellowfin Tuna.

Table 6

Estimates of the batch fecundity (BF) and the relative batch fecundity (BFrel) of Yellowfin Tuna (*Thunnus albacares*) reported for previous studies in different areas of Pacific and Indian Oceans. Values are expressed in millions for BF and in oocytes per gram of gonad-free weight for BFrel.

Studies	Area	BF	BFrel
Hassani and Stéquert (*see fn. 5 in the text*)	Western Indian Ocean	0.50–8.00	–
Timochina and Romanov (*see fn. 3 in the text*)	Western Indian Ocean	3.27	–
Schaefer 1996	Eastern Pacific Ocean	1.57	68.0
Schaefer 1998	Eastern Pacific Ocean	2.50	67.3
Itano (*see fn. 2 in the text*)	Hawaii area	3.45	63.5
Itano[2]	Equatorial western Pacific	2.16	54.7
Sun et al. (*see fn. 6 in the text*)	Western Pacific Ocean	2.71	62.1

Acknowledgments

We thank X. Salaberria for his work in processing samples. We greatly appreciate the assistance of J. Murua, G. Ocio, and A. Sánchez for sample collections on board the purse seiner. This research benefited from the financial support of the Department of Agriculture, Fisheries and Food of the Basque Government, and the Pesquería Vasco Montañesa S.A. (PEVASA) fishing company. This work was partly funded by a grant from the Fundación Centros Tecnológicos Iñaki Goenaga to Iker Zudaire for his doctoral work. We also are grateful for the contribution received from EMOTION project (ANR JSV7 007 01). This paper is contribution no. 628 from AZTI-Tecnalia (Marine Research Department).

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