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Size at Sexual Maturity of Bigeye Tuna *Thunnus obesus* (Perciformes: scombridae) in the Tropical Waters: a Comparative Analysis

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Abstract

The size and proportions of bigeye tuna reach maturity in the stock is an important reference for decision making in fisheries management. The size at 50% sexual maturity (L_{50}) of bigeye tuna, *Thunnus obesus*, was investigated, the data was taken from the 1,042 sampling fish caught from the tropical Atlantic Ocean (TAO), 1,313 from the west-central tropical Indian Ocean (WCTIO) and 391 from the Eastern and Central Tropical Pacific Ocean (ECTPO) and five common models were used for estimating the parameter L_{50}. The results showed that the observed minimum fork length that attained sexual maturity for female (male) bigeye tuna in the TAO, female (male) bigeye tuna in the WCTIO, and female bigeye tuna in the ECTPO to be around 104 cm (108 cm), 110 cm (110 cm) and 94 cm, respectively. The estimated L_{50} of female bigeye tuna in the TAO, the WCTIO and the ECTPO were 117.7 cm, 119.3 cm and 117.5 cm respectively. However, for male bigeye tuna, the estimated L_{50} in the TAO (119.5 cm) was larger than that in the WCTIO (117.7 cm). The Akaike's information criterion showed that the Lysack's (1980) model can be accepted as the best model for estimating L_{50} of bigeye tuna.

Keywords: Bigeye tuna, *Thunnus obesus*, size at sexual maturity, reproduction

Tropikal Sulardaki İrigöz Orkinos *Thunnus obesus* (Scombridae: Perciformes) Balıklarının Cinsel Olgunluk Boyuna Erişme Oranı: Karşılaştırmalı Bir Analiz

Özet

İrigöz orkinos stokları konusunda balıkçılık yönetiminde karar vermek için stoktaki cinsel olgunluğa erişen balıkların oranı ve balık büyüklüğü önemli bir referanstır. İrigöz orkinosun, *Thunnus obesus* %50'sinin cinsel olgunluğa (L_{50}) geldiği büyüklüğü araştırıldı. Tropikal Atlantik Okyanusu (TAO), yakalanan balıklardan 1.042 adet örnekleme alındı. Ayrıca veri toplanan orta-batı tropik Hint Okyanusu (WCTIO) 1,313 adet ve Doğu ve Orta Tropikal Pasifik Okyanusu (ECTPO) 391 adet balıktan elde edilen verilerde beş ortak modelden parametre L_{50} tahmin etmek için kullanılmıştır. İrigöz orkinoslarda cinsel olgunluğa ulaştığı asgari çatal boy sırasıyla ECTPO bölgesinde dişi (erkek) balıklarda 104 cm (108 cm) olarak; TAO bölgesinde ise dişi (erkek) balıklarda 110 cm (110 cm) ulaştığı tespit edilirken, WCTIO bölgesinde dişilerde 94 cm olarak saptanmıştır. İrigöz orkinosların dişi bireylerinde L_{50} değeri ise TAO, WCTIO ve ECTPO bölgelerinde sırasıyla 117,7 cm, 119,3 cm ve 117,5 cm tahmin edilmiştir. Ancak erkek bireylerde, L_{50} değeri TAO (119,5 cm) bölgesinde WCTIO (117,7 cm) bölgesine göre daha büyük hesaplanmıştır. Sonuç olarak Akaike'nin bilgi kriteri Lysack (1980) modeli İrigöz orkinos balıklarında L_{50} değerini tahmin etmek için en iyi model olarak kabul edilebilir.

Anahtar Kelimeler: İrigöz orkinos, *Thunnus obesus*, cinsel olgunluk boyu, üreme.

Introduction

Bigeye tuna (*Thunnus obesus* Lowe, 1839) is a major target species for the commercial fishery in the tropical and subtropical water of the Atlantic, Indian, and Pacific Oceans (45°N - 43°S) along a temperature range of 13–29°C (Collette and Nauen, 1983) and also is the target species of Chinese tuna longline fishing fleets since the late 1980s (Huang and Miao, 2003; Zhu and Xu, 2006; Zhu *et al.*, 2007) and the annual catch reached 25,000 t in 2006.

An individual tuna can physiologically initiate full gametogenesis in response to the appropriate environmental cues until it reach a minimum size or age (Schaefer, 2001). The size and/or age at which a certain fraction (e.g., 50%) of a population of tuna species reaches maturity are an important parameter of fish life history (Chen and Paloheimo, 1994). In order to estimate the parameter (L_{50}), many methods were used in the previous literatures, from the

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Gompertz's (1825) method dating back to Richards (1959) and to the recent multivariate model by White *et al*. (2002). There may be large differences in the estimated L_{50} using different methods (Trippel and Harvey, 1991).

Studies on the reproductive biology of the bigeye tuna were recently done in fish caught both in the Pacific (Yuen, 1955; Sun *et al.*, 1999; Schaefer *et al.*, 2005; Farley *et al.*, 2006; Sun *et al.*, 2006), Indian (Nootmorn, 2004; Ariz *et al.*, 2006) and Atlantic Oceans (Sakamoto, 1969; Matsumoto and Miyabe, 2002; Miyabe, 2003; Sarralde *et al.*, 2003). However, there are still large uncertainties about the population biology of bigeye tuna (Schaefer, 2001; Schaefer *et al.*, 2005). The bigeye tuna of Eastern Pacific Ocean (EPO) and Western and Central Pacific Ocean (WCPO) is being overfished and Regional Fisheries Management Organizations (RFMOs) are making progress towards having or does have conservation measures in place to ensure the stock's recovery to a level at or above that which can produce Maximum Sustainable Yield (MSY) (ISSF, 2009). There also is few information or study on comparing the size at sexual maturity of bigeye tuna inhabiting the Atlantic, Indian, and Pacific Ocean till now and lack accurate information on the size-specific reproductive characteristics of bigeye tuna in the EPO (Schaefer, 2001) and Indian Ocean. So the objectives of this study were to compare the differences on size at sexual maturity of bigeye tuna among different oceanic regions and therefore for making informed fisheries management decisions, another objective is to identify the best model for estimating the size at sexual maturity of bigeye tuna.

Materials and Methods

Field Sampling and Processing

The gonads were collected randomly by the experienced fishery observers in Chinese longline fleets from the TAO, the WCTIO and the ECTPO on a daily basis. In the TAO, gonads were collected by longliner during October 2002 to April 2006. In the WCTIO, gonads were collected by longliner during January 2003 to December 2005. In the ECTPO, gonads were collected by longliner during February through November 2006 (Figure 1). Gonads were sampled from 1,042 fishes (female, 413; male, 629) in the TAO, 1,313 fishes (female, 572; male, 741) in the WCTIO, and 391 female fishes in the ECTPO (Table 1). Random samples were drawn with respect to different fish size.

Fork length (FL) was measured with calipers to the nearest millimeter and dressed weight (gilled, gutted, part of head off, and fins off) was measured with an electronic balance to the nearest 0.1 kg. The gonads were removed and weighted to the nearest gram by using an electronic balance. Sex was determined by macroscopic observation of the

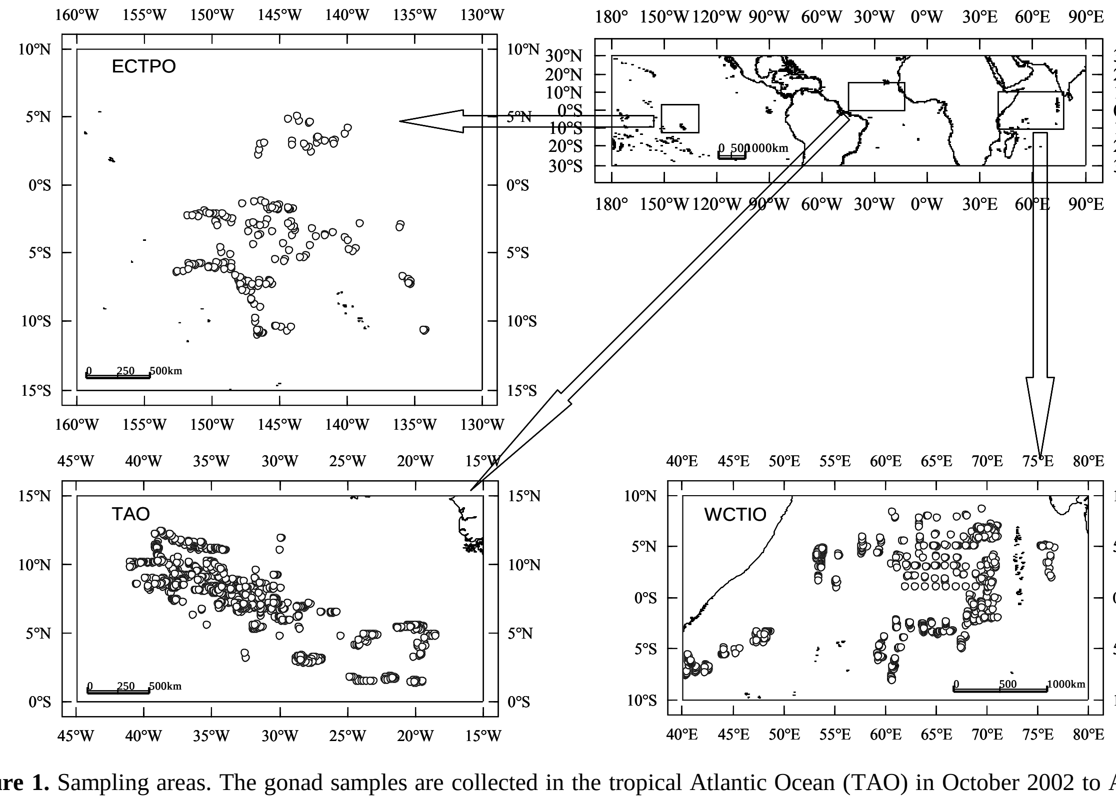

Figure 1. Sampling areas. The gonad samples are collected in the tropical Atlantic Ocean (TAO) in October 2002 to April 2006, west-central tropical Indian Ocean (WCTIO) in January 2003 to December 2005 and Eastern and Central tropical Pacific Ocean (ECTPO) in February to November 2006.

Table 1. The number of gonad samples and size range of bigeye tuna in the Atlantic, Indian and Eastern Pacific Oceans

Month	FL range (cm)					Number of gonad sample				
	Female			Male		Female			Male	
	Atlantic	Indian	Eastern Pacific	Atlantic	Indian	Atlantic	Indian	Eastern Pacific	Atlantic	Indian
2	105.0-188.0	82.0-169.0	112.0-184.0	102.6-185.2	99.1-201.0	37	42	5	42	66
3	102.8-177.0	87.0-176.0	98.0-192.0	87.2-176.3	94.0-190.0	47	92	24	57	125
4	90.0-177.1	90.0-178.0	85.0-189.0	100.1-180.2	89.0-188.0	162	149	97	271	134
5	99.5-162.5	84.0-171.0	92.0-164.0	101.5-169.5	90.0-189.5	59	122	55	84	141
6	101.6-164.4	86.0-172.0	95.0-174.0	106.0-182.7	69.0-199.0	55	76	43	78	129
7	112.3-165.5	-	94.0-161.0	115.1-164.0	-	6	-	43	10	-
8	-	-	102.0-184.0	-	-	-	-	19	-	-
9	-	88.0-170.0	87.0-187.0	-	97.0-167.0	-	28	29	-	65
10	95.0-169.0	92.0-148.0	96.0-182.0	103.5-176.0	103.0-165.0	25	32	57	38	35
11	93.5-157.0	103.0-152.0	96.0-150.0	86.0-160.5	100.0-164.0	22	31	19	49	46

"-" signify no data available.

gonads. The stages of sexual maturity were also determined.

The mature Stage for Male and Female Bigeye Tuna Based on Visual Observations

The ovary of bigeye tuna is considered asynchronous because oocytes in various developmental stages are present in the ovary simultaneously (Wallace and Selman, 1981). We identify the stages of gonads with visual observations for the limitations of in situ condition. For each ovary, the oocytes in the most-developed mode were classified as: (1) Ⅰ- Undeveloped stage; (2) Ⅱ - Early developing stage; (3) Ⅲ - Later developing stage; (4) Ⅳ - Mature stage; (5) Ⅴ - Spawned stage; (6) Ⅵ - Spent stage (Sun *et al.*, 2006). The similar classification criterion (6 stages) was conducted to the testis of bigeye tuna.

Size at 50% Sexual Maturity

The size at which 50% of fish were sexually mature was estimated for reproductively active fish (Stages Ⅳ–Ⅵ) per 5 cm size-class by fitting a model of the below form.

1. Richards' (1959) model (Model 1): The Richards (1959) function, with P_∞=1, was fitted to the non-transformed data set of proportions mature for bigeye in each 5 cm interval, using a weighted nonlinear regression procedure:

$$P_L = [1-(1-\mathrm{m})e^{-k(L-L_{50})}]^{1/(1-m)}$$

where P_L is the proportion mature at length L, m, k and L_{50} were the parameters to be estimated. The weighting employed consisted of the reciprocal of the variance about the proportions at each length interval.

2. Lysack's (1980) model (Model 2):

$$P_L = \frac{G}{1+e^{-\delta(L_{50}-L)}}$$

where, P_L is the proportion of the mature fish at length L, G is maximum attainable proportion of the mature fish in the analysis; L_{50} and δ (the rate at which maturity is attained) are the parameters to be estimated. For most fish populations in nature, all individuals will attain maturity after a specific length (Chen and Paloheimo, 1994). In this case, parameter G is equal 1.

3. Bakhayokho's (1983) model (Model 3):

$$P_L = \frac{1}{1+e^{a+bL}}$$

where P_L is the estimated proportion of mature individuals at fork length L, and a and b are parameters that define the shape and position of the fitted curve. The predicted L_{50} maturity was calculated as: $L_{50} = -a/b$.

4. Gompertz's (1825) model (Model 4):

$$P_L = e^{-e^{-\theta(L-L_{50})}}$$

The Richards, logistic, and Gompertz functions (Seber and Wild, 1989), with P_∞=1, were fitted to the non-transformed combined data for proportions mature in each 5 cm interval, using a weighted nonlinear regression procedure. However, Gompertz function was the best fit with the fewest number of parameters, based on an approximate F-ratio statistic (Schnute, 1981).

5. White's (2002) model (Model 5):

$$P_L = \frac{1}{1+e^{[-\ln(19)\frac{(L-L_{50})}{(L_{95}-L_{50})}]}}$$

where are L_{50} and L_{95} are constants and to be estimated, which are more meaningful to the biologist than those of the traditional equation (White *et al.*, 2002) and *ln* is the natural logarithm.

The above parameters were estimated by nonlinear minimization of a negative binomial log-likelihood of the form (Maartens and Booth, 2005; Rutaisire and Booth, 2005)

$$-\ln L = \sum_{L} y_L \ln\left(\frac{P_L}{1-P_L}\right) + n_L \ln(1-P_L)$$

where y_L is the observed numbers of fish mature in a total of n_L fish sampled in length class L. Maximum-likelihood estimates of the parameters were obtained using the routine SOLVER in the Microsoft Excel and calculating the likelihood of immature and mature individuals as 1- P_L and P_L Microsoft, Redmond, WA).

In order to examine the best model for expressing size at 50% sexual maturity of bigeye tuna, the Akaike's information criterion (*AIC*) (Akaike, 1973) is used to assess which model is the best model for estimating the size at sexual maturity of bigeye tuna:

$$AIC = 2(K - \ln L),$$

where K is the sum of the number of parameters among the models. The best model is selected based on the smallest AIC value. In all cases, model selection was aided by conducting a critical examination of the assumptions and hypothesis of all the models and by selecting those that were considered more appropriate to the data.

Results

The observed minimum size at sexual maturity for female (male) bigeye tuna in the TAO, female (male) bigeye tuna in the WCTIO, and female bigeye tuna in the ECTPO to be around 104 cm (108 cm), 110 cm (110 cm) and 94 cm fork length, respectively.

L_{50} was calculated for female and male bigeye tuna in the TAO using 5 models. The similar results (female, L_{50} = 117.7 cm; male, L_{50} = 119.5 cm) can be concluded using Lysack (1980), White (2001) and Bakhayokho's (1983) model. The maximum estimated result is derived from the method of Richards' (1959) (female, L_{50} = 119.8 cm; male, L_{50} =118.3 cm) and the minimum is from Gempertz' model (female, L_{50} = 108.9 cm; male, L_{50} = 111.5 cm). For the maturation rate (the rate that fishes were attained maturity), the maximum and minimum of female bigeye tuna is 0.071 cm^{-1} (Richards' (1959) model) and 0.049 cm^{-1} (Gompertz's model), respectively, male bigeye tuna, however, is 0.072 cm^{-1} (Lysack's (1980) model) and 0.055 cm^{-1} (Gompertz's model), respectively. Compared the 5 models, the minimum *AIC* value is 75.793 from Lysack's (1980) and can be accepted as the best growth model (Table 2).

We can also draw the same conclusions from the

Table 2. Comparison of parameters and Akaike's information criterion (AIC) for the models on size at 50% sexual maturity of bigeye tuna, *Thunnus obesus*, in the tropical waters

Study area	Sex	Model	L_{50} (cm)	*AIC*	δ	k	m	θ	L_{95} (cm)
TAO	Female	Model 1	119.8	77.727	-	0.071	2.342	-	-
		Model 2	117.7	75.793	0.066	-	-	-	-
		Model 3	117.7	77.793	-	-		-	-
		Model 4	109.0	78.211	-	-	-	0.049	-
		Model 5	117.7	77.793	-	-	-	-	162.2
	Male	Model 1	118.3	71.745	-	0.069	1.813	-	-
		Model 2	119.5	69.799	0.072	-	-	-	-
		Model 3	119.3	84.443	-	-	-		-
		Model 4	111.5	71.914	-	-	-	0.055	-
		Model 5	119.3	84.443	-	-	-	-	153.9
WCTIO	Female	Model 1	131.8	71.209	-	0.179	5.592	-	-
		Model 2	119.5	69.799	0.085	-	-	-	-
		Model 3	119.3	84.443	-	-	-	-	-
		Model 4	109.8	100.949	-	-	-	0.055	-
		Model 5	119.3	84.443	-	-	-	-	153.9
	Male	Model 1	122.4	77.591	-	0.086	2.826	-	-
		Model 2	117.7	76.412	0.072	-	-	-	-
		Model 3	117.7	78.412	-	-	-	-	-
		Model 4	108.8	81.421	-	-		0.054	-
		Model 5	117.7	78.412	-	-	-	-	158.4
ECTPO	Female	Model 1	-	-	-	-	-	-	-
		Model 2	117.5	62.840	0.088	-	-	-	-
		Model 3	117.5	64.840	-	-	-	-	-
		Model 4	111.8	59.477	-	-	-	0.074	-
		Model 5	117.5	64.840	-	-	-		151.0

L_{50}, size at 50% sexual maturity; δ, the rate at which maturity is attained; k and m, the parameters in the Richards' (1959) model; θ, the parameter in the Gompertz's (1825) model; L_{95}, size at 95% sexual maturity. TAO, Tropical Atlantic Ocean; WCTIO, West and Central Tropical Indian Ocean; ECTPO, Eastern and Central Tropical Pacific Ocean; Model 1, Richards' (1959) model; Model 2, Lysack's (1980) model; Model 3, Bakhayokho's (1983) model; Model 4, Gompertz's (1825) model; Model 5, White's *et al.* (2002) model; "-" signify no data available.

estimation on L_{50} of bigeye tuna in the female (male) bigeye tuna in the WCTIO and female bigeye tuna in the ECTPO (Table 2 and Figure 2).

The L_{50} of female bigeye tuna is lower than male in the TAO, however, the opposite result can be observed to the L_{50} of bigeye tuna in the WCTIO. The L_{50} of female (male) bigeye tuna in WCTIO (TAO) was highest among the three oceanic regions.

Discussion

Nootmorn (2004) estimated L_{50} of bigeye tuna in the eastern Indian Ocean is 88.08 cm (female) and 86.85 cm (male) using Bakhayokho's (1983) model, Farley *et al.* (2003, 2006) reported L_{50} of bigeye tuna in the Australian region from longliner was 102.4 cm (female) and 86.6 cm (male) with Bakhayokho's (1983) model. Schaefer *et al.* (2005) estimated L_{50} of female bigeye tuna in the Eastern and Central Pacific Ocean was 135 cm using the model of Richards' (1959). Regardless of the methodology utilized, most previous studies have reported the minimum size at sexual maturity for female bigeye to be around 100 cm, which is similar to the finding in the present study

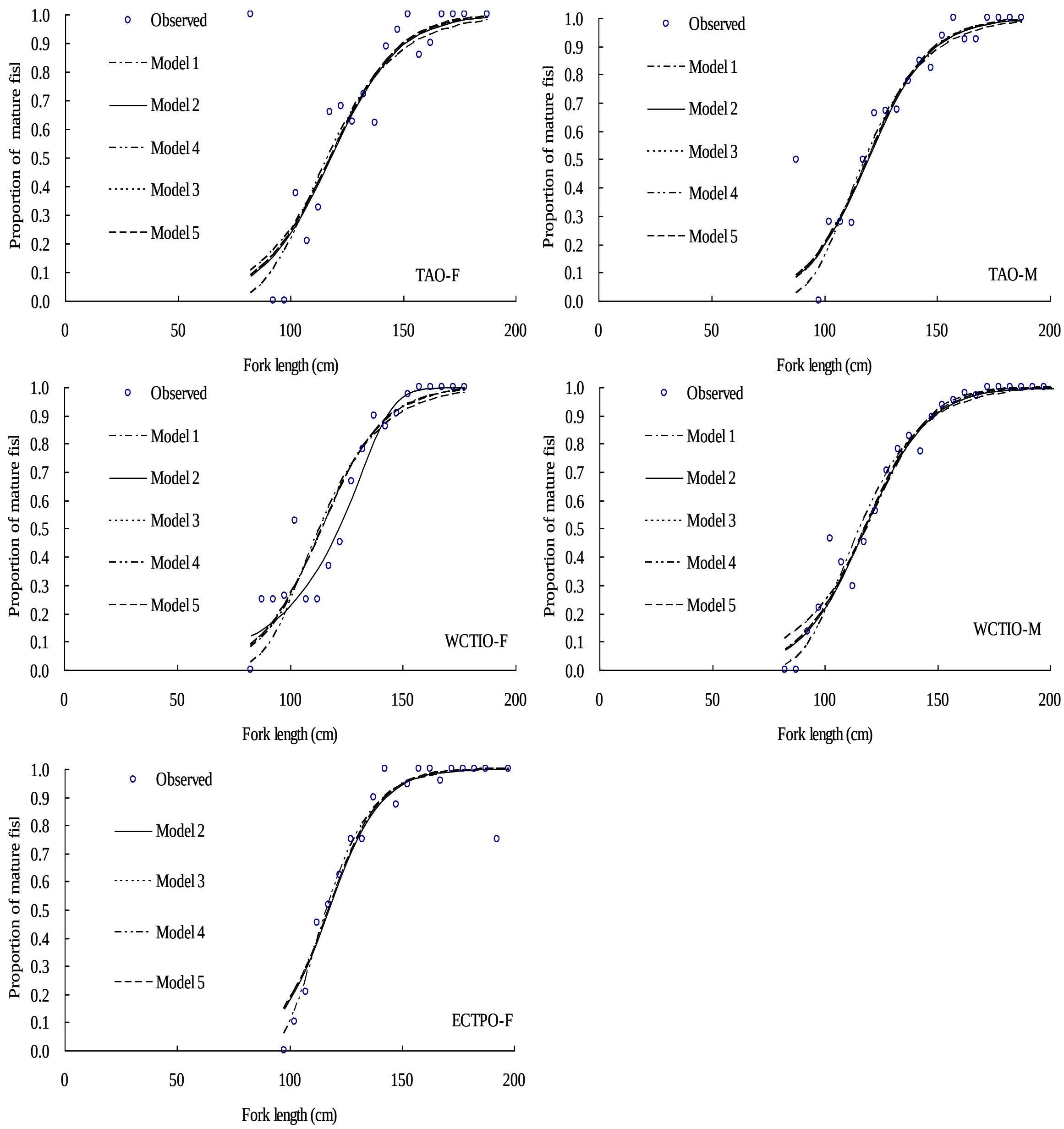

Figure 2. Size at 50% sexual maturity of bigeye tuna, *Thunnus obesus*, in the tropical Atlantic, west-central tropical Indian, and east-central tropical Pacific Ocean. TAO-F (TAO-M), female (male) bigeye tuna in the tropical Atlantic Ocean; WCTIO-F (WCTIO-M), female (male) bigeye tuna in the west-central tropical Indian Ocean; ECTIO-F, female bigeye tuna in the Eastern and Central tropical Pacific Ocean; Model 1, Richards' (1959) model; Model 2, Lysack's (1980) model; Model 3, Bakhayokho's (1983) model; Model 4, Gompertz's (1825) model; Model 5, White's *et al.* (2002) model.

(Table 3). The AIC values indicate that the best model for estimating the size at sexual maturity of bigeye tuna is Lysack's (1980) model (Table 3).

The size at sexual maturity of bigeye tuna is an important life history parameter that has been estimated in previous studies of sexual maturity but inadequately. The apparent size at first maturity is often reported, however, which is misleading regarding the reproductive potential of a population and inappropriate for decision making for fisheries management and stock assessments (Schaefer, 2001). The current study has derived a functional relationship between the estimated proportion mature and length of bigeye tuna. Whereas the minimum observed size at sexual maturity for female bigeye in the TAO, female (male) bigeye tuna in the WCTIO, and female bigeye tuna in the ECTPO to be around 104 cm (108 cm), 110 cm (110 cm) and 94 cm, respectively. The predicted L_{50} for female (male) bigeye in the TAO, female (male) bigeye tuna in the WCTIO, and female bigeye tuna in the ECTPO to be 117.7 cm (119.5 cm), 119.5 cm (117.7 cm) and 117.5 cm using the best model.

The minimum size at first maturity of Pacific bigeye tuna is reported as 91–100 cm by Kikawa (1953). Yuen (1955) also reported minimum size at first maturity, but his results were given in weight (14–20 kg). These two values are equivalent and are supported by the later studies (Kikawa, 1957; 1961; 1962).

For bigeye tuna inhabiting the Atlantic, Indian and Pacific Ocean, Calkins (1980) reported bigeye tuna reached sexual maturity at a size of 100 to 130 cm, when they are about 3 years old. In addition, bigeye tuna had previous reported on L_{50} as 91-100 cm in the Pacific Ocean (Kikawa, 1953; Yuen, 1955). McPherson (1991, 1992) reported L_{50} of bigeye tuna in the Coral Sea to be 100-125 cm in areas fished by handline and by longlines, respectively. The result of stock assessment estimated by International Commission on Conversation Tuna in the Atlantic Ocean (ICCAT) indicated that the age attained maturity was about 3 years and corresponding size was 100 to 120 cm. However, no update information were reported on the L_{50} of bigeye tuna in the Atlantic Ocean (Anonymous, 2005). Based on evaluations of gonad indices Kikawa (1953, 1957, 1961, 1962) reported that very few female bigeye sampled in the Pacific Ocean were mature at less than 100 cm. Yuen (1955) concluded a weight of 14 to 20 kg as the range necessary to attain sexual maturity and reported a similar minimum length at maturity, based on gonad indices, for female bigeye sampled from the central and western equatorial Pacific. Kume (1969) recorded the minimum size for spawning as 92 cm in fork length, while Kume and Joseph (1966) estimated that bigeye tuna in the eastern Pacific reached maturity at 100 to 130 cm on the basis of gonad indices and that the minimum length at maturity for female bigeye sampled from the EPO was about 100 cm. McPherson (1988) and Nikaido *et al.* (1991) noted that some fish as small as 100 cm long could be mature. McPherson (1991, 1992) reported the minimum size at first maturity in the Coral Sea, based on comparisons of macroscopic and histological classifications, to be 100 and 125 cm in areas fished by handline and by longlines, respectively. The minimum length at maturity based on histological evaluations of ovarian tissues from female bigeye sampled in the western Pacific Ocean was reported to be 100 cm (Sun *et al.*,

Table 3. The size at sexual maturity and minimum observed length at maturity of bigeye tuna in the Pacific, Indian and Atlantic Oceans

Areas	L_{50} (cm)			L_m (cm)			Sources
	Female	Male	Unsexed	Female	Male	Unsexed	
Atlantic	-	-	100-120	-	-	-	Anonymous (2005)
	-	-	64(handline)/ 100(longline)	-	-	-	Hisada (1973)
	117.7	119.5	-	104	108	-	The present study
Indian	88.08	86.65	-	-	-	-	Nootmorn (2004)
	102.40	86.60	-	-	-	-	Farley *et al.* (2003)
	-	-	92	-	-	-	Kume (1962)
	119.5	117.7	-	110	110	-	The present study
Pacific	-	-	91-100	-	-	-	Kikawa (1953)
	-	-	< 100	-	-	-	Kikawa (1962)
	-	-	108(handline)/ 120(longline)	-	-	97(handline)/ 113(longline)	McPherson (1991)
	-	-	100-125	-	-	-	McPherson (1992)
	-	-	91-100	-	-	-	Yuen (1955)
	-	-	-	-	-	99.7	Sun *et al.* (1999)
	-	-	> 100	-	-	-	Nikaido *et al.* (1991)
	135	-	-	-	-	-	Schaefer *et al.* (2005)
	-	-	100-130	-	-	-	Kume and Joseph (1966)
	-	-	102.40	-	-	-	Farley *et al.* (2006)
	117.5	-	-	94	-	-	The present study

L_{50}, size at sexual maturity; L_m, minimum observed length at maturity; "-" signify the value unavailable.

1999). Sun *et al.* (2006) studied the minimum maturity length of bigeye tuna in the WCPO was 99.7 cm based on the histological examination and outside view of gonads.

The smallest mature female reported from the northwestern Pacific Ocean in a relatively recent study was 80 cm and L_{50} was estimated to be 102.4 cm in females (Farley *et al.*, 2003; 2006), which, obviously, were lower the values resulted in the present study (117.5 cm). The classification of mature or immature was also based on macroscopic appearance of the ovaries. It should be well known that life history characteristics of bigeye tuna, including size at maturity, may indicate some geographic variation across the Pacific, considering the limited amount of mixing observed from tagging studies to date (Hampton and Williams, 2005; Schaefer *et al.*, 2005).

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References

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: B.N. Petran and F. Csaaki (Eds.), International Symposium on Information Theory, 2nd edition, Acadeemiai Kiadi, Budapest, Hungary: 267-281.

Anonymous 2005. 2004 ICCAT bigeye tuna year program symposium. Collective Volume of Scientific Papers of ICCAT, 57: 3-60.

Ariz, J., Delgado de Molina, A., Ramos, M.L. and Santana, J.C. 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 2005. http://www.iotc.org/files/proceedings/2006/wptt/IOTC-2006-WPTT-05.pdf (accessed November 28, 2009).

Bakhayokho, M. 1983. Biology of the cuttlefish *Sepia officinalis hierredda* off the Senegal coast. FAO Fish Technical Paper, 231: 204-263.

Calkins, T.P. 1980. Synopsis of biological data on the bigeye tuna, *Thunnus obesus* (Lowe, 1839), in the Pacific Ocean. In: W.H. Bayliff (Ed.), Synopses of biological data on eight species of scombrids. Inter-American-Tropical-Tuna-Commission Special Report, 2: 219-59.

Chen, Y. and Paloheimo, J.E. 1994. Estimating fish length and age at 50% maturity using a logistic type model. Aquatic Science, 56: 206-219.

Collette, B.B. and Nauen, C.E. 1983. FAO Species Catalogue. Scombrids of the World. An Annotated and Illustrated Catalogue of Tunas, Mackerels, Bonitos and Related Species Known to Date. FAO Fish Synop 2, Rome, 137 pp.

Farley, J., Clear, N., Leroy, B., Davis, T. and Mcpherson, G. 2003. Age and Growth of Bigeye Tuna (*Thunnus obesus*) from the Eastern and Western AFZ. Report No. 2000/100. CSIRO Marine Research. Hobart Tamania, Australia, 93 pp.

Farley, J.H., Clear, N.P., Leroy, B., Davis, T.L.O. and McPherson, G. 2006. Age, growth and preliminary estimates of maturity of bigeye tuna, *Thunnus obesus*, in the Australian region. Marine and Freshwater Research, 57: 713-724.

Gompertz, B. 1825. On the nature of the function expressive of the law of human mortality. Philosophical Transactions of the Royal Society of London, 115: 513–585.

Hampton, J. and Williams, P. 2005. A description of tag-recapture data for bigeye tuna (*Thunnus obesus*) in the western and central Pacific Ocean. Collective Volume of Scientific Papers of ICCAT, 57: 85-93.

Huang, X.C. and Miao, Z.Q. 2003. Distant Waters Tuna Fishery. Shanghai Science and Technology Press, Shanghai, 451 pp. (in Chinese)

ISSF. 2009. Tuna Sustainability Matrix. http://www.iss-foundation.org/tsm (accessed May 31, 2009).

Kikawa, S. 1953. Observations on the spawning of the big-eyed tuna (*Parathunnus mebachi* Kishinouye) near the sourthern Marshall Islands. Contribution of the Nankai Regional Fisheries Research Laboratory, 1-10.

Kikawa, S. 1957. The concentrated spawning area of bigeye tuna in the western Pacific. Nankai Regional Fisheries Research Laboratory Report, 5: 145-157.

Kikawa, S. 1961. The group maturity of bigeye tuna *Parathunnus mebachi* (Kishinouye) in the spawning areas of the Pacific. Nankai Regional Fisheries Research Laboratory Report, 13: 35-46.

Kikawa, S. 1962. Studies on the spawning activity of Pacific tunas, *Parathunnus mebachi* and *Neothunnus macropterus*, by the gonad index examination. Nankai Regional Fisheries Research Laboratory Report, 1: 43-56.

Kume, S. 1969. Ecological studies on bigeye tuna - V. A critical review on distribution, size composition and stock structure of bigeye tuna in the North Pacific Ocean (north of 16°N). Bulletin Far Seas Fisheries Research Laboratory, 1: 57-75.

Kume, S. and Joseph, J. 1966. Size composition, growth and sexual maturity of bigeye tuna, *Thunnus obesus* (Lowe), from the Japanese longline fishery in the eastern Pacific Ocean. Inter-American-Tropical-Tuna-Commission Bulletin, 11: 45-99.

Lysack, W. 1980. 1979 Lake Winnipeg Fish Stock Assessment Program. Manitoba Department of Natural Resources, MS Report No. 80-30, Canada, 118 pp.

Maartens, L. and Booth, A.J. 2005. Aspects of the reproductive biology of monkfish, *Lophius vomerinus*, off Namibia. African Journal of Marine Science, 27: 325-329.

Matsumoto, T. and Miyabe, N. 2002. Preliminary report on the maturity and spawning of bigeye tuna *Thunnus obesus* in the central Atlantic ocean. Collective Volume of Scientific Papers of ICCAT, 54: 246-260.

McPherson, G.R. 1988. Verification of the Postovulatory Follicle Method for Establishing the Spawning Frequency of Yellowfin, Bigeye and Skipjack Tuna in the Coral Sea. Queensland Dep. Primary Industries, Northern Fisheries Res. Center, Technical Report FRB 88/9, Cairns, Australia, 42 pp.

McPherson, G.R. 1991. Reproductive biology of yellowfin tuna in the eastern Australain fishing zone, with special reference to the North-western Coral Sea. Australian Journal of Marine & Freshwater Research, 42: 465-477.

McPherson, G.R. 1992. Assessing Macroscopic and Histological Staging of Yellowfin and Bigeye Ovaries in the North-Western Coral Sea. Inf. Ser. Dep. Primary Ind. (Queensl.) Brisbane, 26 pp.

Miyabe, N. 2003. Recent sex ratio data of the bigeye tuna caught by the Japanese longline fishery in the Atlantic. Collective Volume of Scientific Papers of ICCAT, 55: 2028-2039.

Nikaido, H., Miyabe, N. and Ueyanagi, S. 1991. Spawning time and frequency of bigeye tuna, *Thunnus obesus*. Bulletin Far Seas Fisheries Research Laboratory, 28: 47-73.

Nootmorn, P. 2004. Repoductive biology of bigeye tuna in the Eastern Indian Ocean. IOTC Proceedings, 7: 1-5.

Richards, F.J.A. 1959. A flexible growth functions for empirical use. Journal of Experimental Botany, 10: 290-300.

Rutaisire, J. and Booth, A.J. 2005. Reproductive biology of ningu *Labeo victorianus* (Pisces: Cyprinidae) in the Kagera and Sio Rivers, Uganda. Environmental Biology of Fishes, 73: 153-162.

Sakamoto, H. 1969. Preliminary review on the regional change in size composition, sex-ratio and gonad index of the Atlantic bigeye caught by tuna long-line fishery. Bulletin Far Seas Fisheries Research Laboratory, 1: 49-56.

Sarralde, R., Bard, F.X. and Ahsoy, A. 2003. Consideraciones sobre el sex-ratio de patudo (*Thunnus albacares*) en el Atlántico este tropical, capturado por la flota de cerco. Collective Volume of Scientific Papers of ICCAT, 55: 1951-1953.

Schaefer, K.M. 2001. Reproductive biology of tunas. In: B.A. Block and E.D. Stevens (Eds.), Tuna: Physiology, Ecology and Evolution, Academic Press, San Diego, Fish Physiology, 19: 225-270

Schaefer, K.M., Fuller, D.W. and Miyabe, N. 2005. Reproductive Biology of Bigeye Tuna (*Thunnus obesus*) in the Eastern and Central Pacific Ocean. Inter-American-Tropical-Tuna-Commission Bulletin 23, 31 pp.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. Canadian Journal of Fisheries and Aquatic Sciences, 38: 1128-1140.

Seber, G.A.F. and Wild, C.J. 1989. Nonlinear Regression. John Wiley and Sons Inc., New York, 768 pp.

Sun, C.L., Chu, S.L. and Yeh, S.Z. 1999. Note on the reproduction of bigeye tuna in the western Pacific. Secretariat of the Pacific Community, Ocean. Fish. Prog., Standing Committee on Tuna and Billfish. SCTB-12. BET-4. June 14-23. French Polynesia, Tahiti.

Sun, C.L., Chu, S.L. and Yeh, S.Z. 2006. The Reproductive Biology of Female Bigeye Tuna (*Thunnus obesus*) in the Western Pacific Ocean. WCPFC-SC2-BISWG-WP -1, 22 pp.

Trippel, E.A. and Harvey, H.H. 1991. Comparison of methods used to estimate age and length of fishes at sexual maturity using populations of white sucker (*Catostomus commersoni*). Canadian Journal of Fisheries and Aquatic Sciences, 48: 1446-1459.

Wallace, R.A. and Selman, K. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. American Zoologist, 21: 325-345.

White, W.T., Hall, N.G. and Potter, I.C. 2002. Size and age compositions and reproductive biology of the nervous shark *Carcharhinus cautus* in a large subtropical embayment, including an analysis of growth during pre- and postnatal life. Marine Biology, 141: 1153-1164.

Yuen, H.S.H. 1955. Maturity and Fecundity of Bigeye Tuna in the Pacific. U.S. Fish and Wildlife Service, Special Scientific Report 150, USA, 30 pp.

Zhu, G.P. and Xu, L.X. 2006. General information of tuna fisheries in the Indian Ocean and comments on the development strategy for Chinese tuna fleet. Chinese fisheries economics, 2: 10-12. (in Chinese with English abstract)

Zhu, G.P., Xu, L.X. and Cao, Z. 2007. Summary on exploitation of tuna fishery in the Atlantic Ocean and the future development of Chinese Distant-Water tuna fishing fleet. Ocean development and management, 24: 12-17. (in Chinese with English abstract)