www.trjfas.org
ISSN 1303-2712
*Turkish Journal of Fisheries and Aquatic Sciences 17: 353-361 (2017)* DOI: 10.4194/1303-2712-v17_2_14

**PROOF**

RESEARCH PAPER

# Growth and Maturity of *Carcharhinus dussumieri* (Muller and Hellen, 1839) in the Persian Gulf and Oman Sea

**Hadi Raeisi[1], Ehsan Kamrani[2], Carl Walter[3], Rahman Patimar[1], Iman Sourinejad[2]**

[1] Gonbad, fisheries, Gorgan, Iran, Islamic Republic Of
[2] Hormozgan, fisheries, Bandar Abas, Iran, Islamic Republic Of
[3] The University of British Columbia, 2. Institute for the Oceans and Fisheries, Vancouver, Canada

* Corresponding Author: Tel.: +90.312 5961688 ; Fax: +90.312 3185298 ;
E-mail: spulatsu@agri.ankara.edu.tr

Received 30 May 2016
Accepted 04 October 2016

## Abstract

This study aimed to estimate the growth pattern and to determine age at maturity ($Lm_{50}$) and longevity of white cheek shark, *Carcharhinus dussumieri* (Muller and Hellen, 1839) during 2014 and 2015. This species is being severely exploited in the Persian Gulf and Oman Sea, so growth, maturity and diet will be critical for stock assessments and management advice. Longevity estimates based on vertebral ageing were 8 and 13 years for male and female of *C. dussumieri.* Results indicated a Gompertz growth model and a logistic growth model for females and males, respectively. The obtained curve revealed a sigmoid relation between clasper length and total length of the shark. Females matured from 60 to 68 cm and their mean maturity size was 64.17 cm. Male *C. dussumieri* matured within a similar size range (61-68 cm) with mean maturity size of 63.14 cm.

*Keywords*: White cheek shark, maturity size, Gompertz, logistic, Persian Gulf, Oman Sea **.**

## Introduction

The family Carcharhinidae with 12 genera and 48 species is the third richest shark family in species diversity. Additionally, this family has the highest biomass and species richness in tropical areas (Fischer and Bianchi, 1984). The genus *Carcharhinus* with 29 species is dominantly distributed in temperate and warmer zones (Fischer and Bianchi, 1984). In the west part of the Indian Ocean, 21 species of the genus *Carcharhinus* live of which 13 species are also reported in the Persian Gulf and the Oman Sea (Carpenter *et al*., 1997).

More than 10 species of *Carcharhinus* inhabits in Iranian waters of the Persian Gulf (Hormozgan Province), amongst which white cheek shark, *Carcharhinus dussumieri* (Muller and Hellen, 1839) is also found throughout the Persian Gulf (Carpenter *et al*., 1997). Sharks are slow-growing organisms with a few newborns in every pregnancy and play an important role in the inhabiting ecosystem (Cortes, 1999؛ Gelsleichter *et al*, 1999؛Stevens *et al*., 2000 ).

Understanding the life cycle and biology of these Condrichthyans is integral to their conservation and successful fisheries management which could be applied in quantitative assessment of the population size. For instance, if the relations amongst length, age, body mass, fecundity and sexual maturity are accurately recognised, length-and age-structured models can be used in population dynamics modelling (Punt *et al*., 2000; Aires-da-Silva and Gallucci 2007). Effective management of Chondrichthyans is particularly important, as many species often have biological characteristics (e.g. slow growth, low fecundity), implicating that only a relatively small proportion of the population can be sustainably harvested annually (Walker *et al*., 1998).

Studies are already indicating that regional elimination of sharks from the ecosystem can cause disastrous effects such as a considerably increased abundance of some crustacean, fish and sea mammals which would led to other species to be constrained, trophic cascade effect and finally the collapses of the whole ecosystem (Ward and Myers 2005, Myers *et al*. 2007). One pound of dried shark fins is commonly retailed at US$ 300. As a one-milliard dollar industry, this vast market is not managed or monitored properly (http://Sharkresearchcommittee.com).

During a few recent years, the annual shark catch has been increasing rapidly along the Iranian waters of the Persian Gulf and the Oman Sea. Stocks of white cheek shark seem to be plentiful, but there are some concerns about its overexploitation. Like most of fish stocks in the Persian Gulf, there is a lack

© Published by Central Fisheries Research Institute (CFRI) Trabzon, Turkey
in cooperation with Japan International Cooperation Agency (JICA), Japan

of information about white cheek shark stocks. Therefore, identifying the growth patterns of *Carcharhinus* in order to assess their impacts in marine ecosystems in the Persian Gulf is necessary.

Despite the commercial and ecological importance of the white cheek shark, our current knowledge on its life history in the Persian Gulf and the Oman Sea is limited to a single study on its reproductive biology (Asadi, 2001). Hence, due to the lack of information on growth and $Lm_{50}$ of the white cheek shark in the Persian Gulf and Oman Sea, it is significant to achieve a better understanding of the species´ status in the local marine ecosystem, especially in terms of its fishing condition in this area. In the present study, we investigated the growth rate and $Lm_{50}$ the white cheek shark in order to determine the feeding preferences of this species in the Persian Gulf.

## Materials and Methods

Sampling was conducted in the Persian Gulf waters during two years from December 2012 to June 2014 (Figure 1). For growth calculation and gonad description, 605 shark samples including 289 females and 316 males which were caught by mid water trawl and gillnet were analyzed.

### Vertebral Processing and Growth Analysis

From the anterior part of the vertebral column, somewhere between the gills and the first dorsal fin, a section of five vertebrates was removed and kept frozen. Using a scalpel, neural and hemal arches together with soft tissue were removed and only the vertebral centra left behind. Then, centra were soaked in a solution of % 5 sodium hypochlorite (bleach) for ~30 min to remove the remaining soft tissues. Thereafter, they were rinsed thoroughly under tap water and placed in an oven at 60°C for 24 h.

The sectioned centera were examined under a dissecting microscope using transmitted light (Figure 2). Determination of the shark´s age was conducted by counting the pairs of transparent and translucent growth bands which was deposited on the corpus calcareum (Cailliet and Goldman, 2004). The birth mark was recognizable by an angle shift on the corpus calcareum.

Prior to aging all centra, a random subsample of the vertebrae was read by two experts to ensure that an agreement in interpreting the banding pattern was achieved. Then, one of the readers examined the whole centers twice. The precision between and within readers was evaluated by the method of Chang (1982), as the coefficient of variation (CV) and percentage of agreement was checked by the method of Goldman and Musick (2006). The bias between and within readers was statistically calculated using a test of symmetry based on Bowker's test (Evans and Hoenig, 1998).

An information-theoretic, multi-model inference (MM) approach was applied for growth modeling (Burnham and Anderson, 2001; Katsanevakis and Maravelias, 2008). Models included a three-parameter version of the von Bertalanffy growth equation (VB), a three-parameter version of the Gompertz function (GOM) and logistic growth curve (LOG). Each model suggests an alternative hypothesis for growth and, in each case, an asymptotic growth was assumed. The three applied models were as the following. Length-weight relationship was estimated for males and females of white cheek shark (Table 1).

(1) Von Bertalanffy (VB):$L_t = \beta_2 + (\beta_1 - \beta_2)(1 - \exp(-\beta_3 t))$

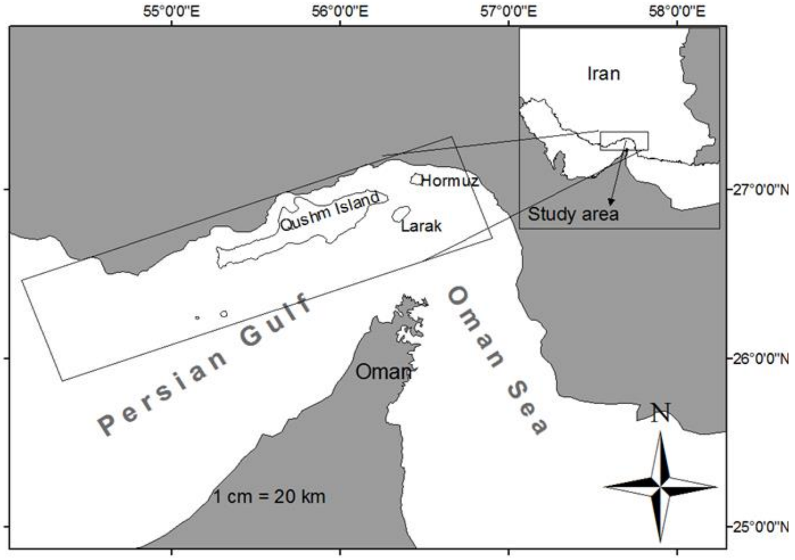

**Figure 1.** Study area of *C. dussumeiri* by trawl and gill net in the northern Persian Gulf

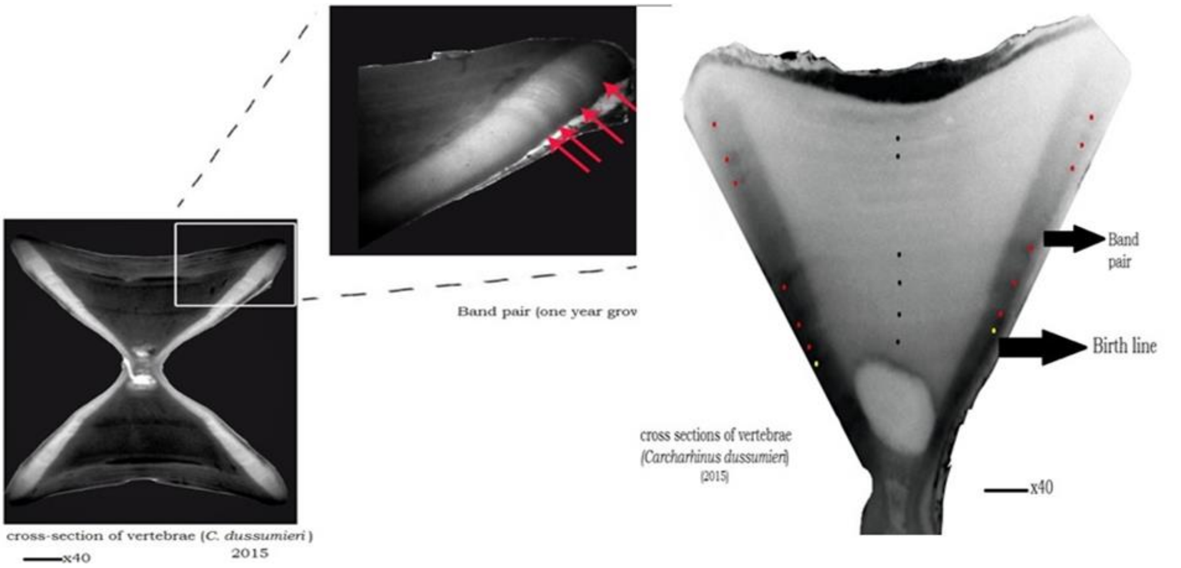

**Figure 2**. Cross-section of the vertebrate in a 6-year old white cheek shark.

**Table 1**. Descriptive statistics and length-weight relationships parameters for males and females of *C. dussumieri*, n: sample size, Min: minimum, Max: maximum, *a* and *b*: constant parameters in equation $W = aL^b$

| | | Length (cm) | | *WLR* parameters and statistics | | |
|---|---|---|---|---|---|---|
| Genus | n | Min | Max | *a* | *b* | $r^2$ |
| Male | 316 | 41.0 | 106 | 0.0031 | 3.105 | 0.985 |
| Female | 289 | 40.6 | 121 | 0.0024 | 3.142 | 0.982 |

Where $L_t$ is length as function of time, $\beta_1$: $L_\infty$ (cm), $\beta_2$: $L_0$ (cm) and $\beta_3$: $k$ (years$^{-1}$).

(2) Gompertz (GOM):

$$L_t = \beta_2 exp\left(ln\frac{\beta_2}{\beta_1}\right)(1-\exp(-\beta_3 t)) \quad (3)$$

Where $L_t$ is length as function of time, $\beta_1$: $L_\infty$ (cm), $\beta_2$: $L_0$ (cm) and $\beta_3$: $k$ (years$^{-1}$).

(4) Logistic (LOG): $$L_t = \frac{\beta_1\beta_2\exp(\beta_3)}{\beta_1+\beta_2(\exp(\beta_3 t)-1)}$$

Where $L_t$ is length as function of time, $\beta_1$: $L_\infty$ (cm), $\beta_2$: inflection of point; and $\beta_3$: $k$ (years$^{-1}$).

Models were fitted by the method of Maximum Likelihood in statistical package Excel (Ver. 2013) with VBA programming language (Haddon, 2011).

Models performance relative to each other was checked using Akaike's Information Criteria (AIC). The model with the least AIC ($AIC_{min}$) was chosen as the best model, $AIC_{min}$. AIC differences was calculated as $\Delta_{AICi} = AIC_i - AIC_{min}$ and ranked relative to the best model in order to support the remaining models (i=1-3). Models with $\Delta_{AIC}$ of 0 and 2 had a substantial support, whereas those with $\Delta_{AIC}$ of 4 to 7 showed considerably less support. Models with $\Delta_{AIC}$ of > 10 essentially revealed no support (Burnham and Anderson, 2001).

Akaike weights (w) were calculated as the evident weight in favor of the model which is selected as the best mode in a set of candidate models (Burnham and Anderson, 2001).

Approximately 95% confidence interval and the precision in parameter estimation of the best fit and population estimates were derived from 10 000 resampled dataset.

The length-weight relationship was estimated by total length (cm) and total weight (g) according to the following equation (Froese, 2006):

$$W = aL^b$$

### Lm50

As described by Walker (2005), a single index was used for staging maturity in each sex. Determination of maturity was based on clasper condition (C=1-3) in males and uterus condition in females (U=1-7). For statistical analysis, data obtained from maturity-stage was converted to binary format (immature=0, mature= 1). Population estimates of length at maturity were established separately for males and females, using a logistic regression model (Roa *et al* 1999) which was reformulated by Walker (2005) to be biologically meaningful as the following:

$$P(I) = P_{MAX}\left(1 + e^{-\ln(19)\left[\frac{1-\beta_1}{\beta_2-\beta_1}\right]}\right)^{-1}$$

Where $P(I)$ is the proportion of population mature in STL, $I$; $\beta_1$ and $\beta_2$ are fitted parameters corresponding to $l_{50}$ and $l_{95}$, respectively; and $P_{MAX}$ is the asymptote. A generalized linear model with binormal error structure and logit-link function was applied to estimate parameters $\beta_1$ and $\beta_2$. The overall significance of fitted models was tested by comparing the amount of explained deviance relative to null model using Chi-squares tests.

$t_0$ where calculated by Pauly equation (1980):

$$\log-(t_0) = -0.3922 - 0.2752 log\, L_\infty - 1.038 log\, K$$

The weight-age relationship was fitted using the following equation (Haddon, 2011).

$$\hat{w}_t = w_\infty\left[1 - e^{-k[t-t_0]}\right]^b$$

Where $W_\infty$ is the asymptotic weight and b: the slope in length-weight relationship. The following formula was applied to estimate $W_\infty$.

$$W_\infty = aL_\infty^b$$

Growth performance index was measured by the following equation (Gayanilo and Pauly, 1997):

$$\phi = \log K + 2 log\, L_\infty$$

The likelihood ratio test was used to compare growth curve between male and female by the following equation (Haddon, 2011):

$$X_K^2 = -N \times Ln\left[\frac{\sum RSS_i}{RSS_p}\right] = -N \times Ln\left(\frac{RSS_\Omega}{RSS_\omega}\right)$$

Where k is the degrees of freedom, N: total number of observations from both curves combined, $RSS_\Omega$: total sum of squared residuals derived from fitting both curves separately and $RSS\omega$: total sum of squared residuals derived from fitting the curves with one of the hypothesized constraints.

## Results

Totally, 605 samples of white cheek shark were studied for biometric measurements and description of gonadal maturation stages. . Mean length for males and females of *C. dussumieri* were 67.278±0.889 and 71.4±1.13, respectively **.**Results of the present study demonstrated that length-frequency distribution had a significant difference between males and females (N=605, $D_{k.s}$=1.22)(Figure 3).

### Growth

Mean inter-reader percentage agreement (PA) and $PA^{-1}$ year between the first and second read pooled into 50mm length groupings was 56% and 71% for *C. dussumeiri*, whereas Chang's coefficient of variation (CV) was 26.40%. Precision was low though no significant difference was observed between the readers (Bowker's test of symmetry: $X^2$=14, *P*, 0.13).

Vertebrae centra from 260 specimens of *C. dussumeiri* were obtained and read. Total length ranged between 41–106 cm for males (n=140) and 40.6–121 cm for females (n=120). The youngest male and female were zero year and were 29.5 cm. The oldest male was 8 years old with total length of 106 cm while the oldest female was 13 years old with total length of 121 cm.

A strongly asymptotic growth curve was recognized for both sexes of *C. dussumeiri*, with fast growth rates during the five few years of life which rapidly decreases thereafter (Figure 4, Table 2). The most parsimonious model for males in the multi-model analysis of growth was logistic model (Table 2,

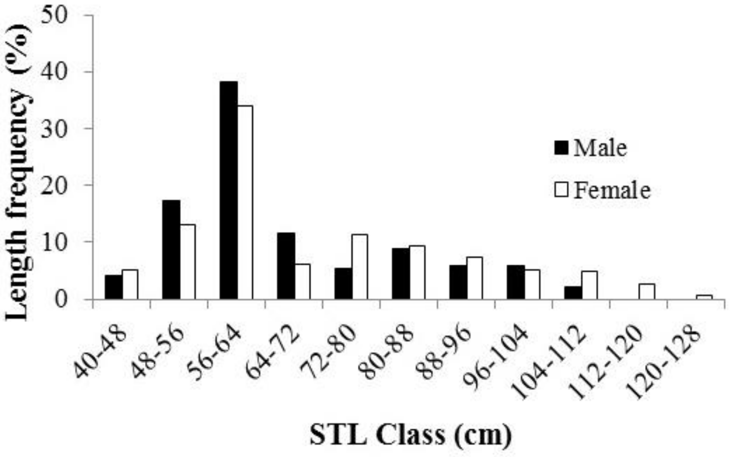

**Figure 3.** Distribution of length frequency in males and females of white cheek shark *Carcharhinus dussumieri.*

$\Delta_{AIC}$=0).

The von Bertalanffy model was also supported by the data to a lesser extent (Table 2, $\Delta_{AIC}$=6.89), whereas the Gompertz model showed little support. The Gompertz model was by far the best, given the data (Table 2, $\Delta_{AIC}$=0), and The von Bertalanffy model was also supported by the data to a lesser extent (Table 2, $\Delta_{AIC}$=6.91).

The best growth curves were acquired by the test of Akaike information test in males and females of white cheek shark. A diagram is represented to compare growth curves estimated in males and females. Comparison of the growth curve between males and females revealed a significant difference ($P<0.05$) (Fig. 4).

As shown in Figure 5, confidence interval for parameters of $L_\infty$, K and $L_0$ was estimated by Maximum Likelihood method.

In addition, the weight-age relationship was estimated in the fish sampled in the present study (Figure 6).

The value of growth performance index $\phi'$ was

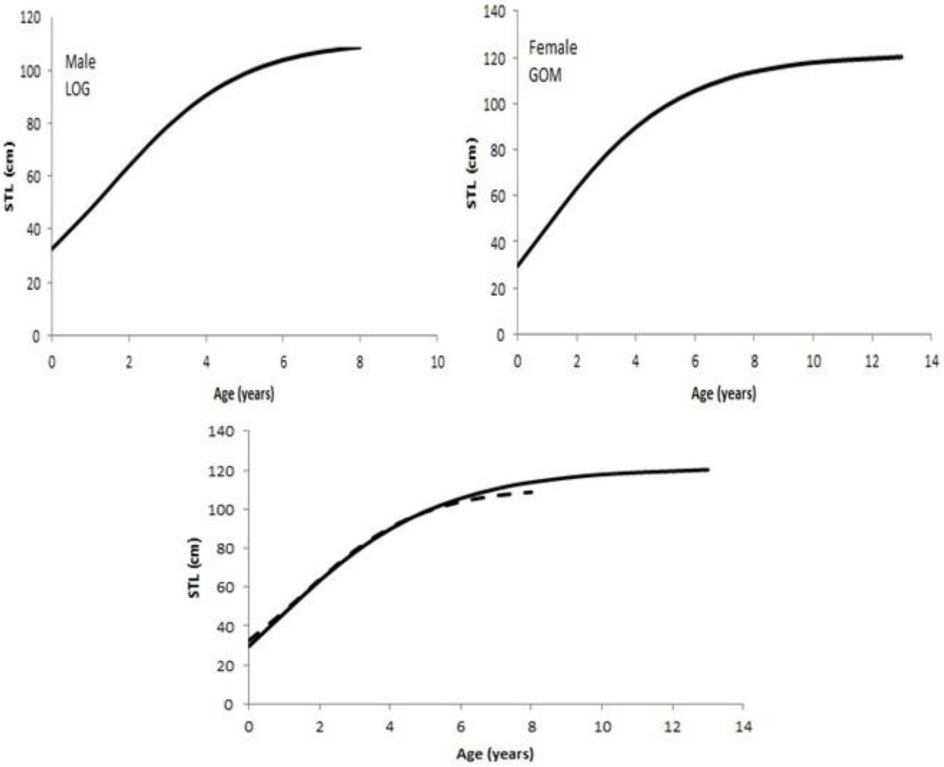

**Figure4.** Length and age curves obtained for white cheek shark *Carcharhinus dussumieri.*

**Table 2**. Comparison of three growth models fit to length-at-age data for *C. dussumeiri.* The best model represented in bold was the one with the lowest value for Akaike's information criterion (AIC). The relative support of other models can be evaluated based on Akaike differences ($\Delta_{AIC}$). Best-fit estimates are given for parameters β1–β3 (with 95% confidence interval).

| Sex | Model | n* | k* | AIC | BIC | $\Delta_{AIC}$ | $\beta_1$ | | $\beta_2$ | | $\beta_3$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Female | VB | 100 | 3 | 38.8 | 36.14 | 12.22 | 126.69 | (123.5-129.6) | 27.06 | (25.1-28.95) | 0.245 | (0.22-0.27) |
| | GOM | 100 | 3 | 26.58 | 23.92 | 0.00 | 121.32 | (120-122.4) | 29.73 | (28.45-30.7) | 0.385 | (0.37-0.398) |
| | LOG | 100 | 3 | 33.50 | 30.84 | 6.91 | 119.51 | (117.9-121.2) | 34.49 | (32.2-35.5) | 0.497 | (0.475-0.51) |
| Male | VB | 98 | 3 | 44.40 | 41.26 | 6.89 | 115.32 | (113.2-117.1) | 28.44 | (27.3-30.2) | 0.29 | (0.265-0.31) |
| | GOM | 98 | 3 | 54.40 | 51.26 | 16.89 | 117.63 | (114.1-120.6) | 29.98 | (26.9-32.6) | 0.453 | (0.423-0.473) |
| | LOG | 98 | 3 | 37.50 | 34.37 | 0.00 | 111.05 | (108.2-114.1) | 32.64 | (28.55-35.02) | 0.589 | (0.543-0.63) |

*n= number of sample
*k = number of parameter

estimated 2.28 and 2.42 for female and male, respectively.

$$\phi = \log 0.38 + 2\log 121.32 = 3.75 \text{ female}$$
$$\phi = \log 0.589 + 2\log 111.05 = 3.86 \text{ male}$$

### $Lm_{50}$

The mature females were found from 60 to 68 cm with maturity size of 64.17 cm length. For males, maturity occurred at length of 61-68 cm and maturity size was estimated 63.14 cm length (Figure 7).

When maturation began, the length of clasper and testicles weight quickly increased which made the clasper rigid. As illustrated in Figure 4, a sigmoid curve was found for the relationship between clasper length and total body length. Clasper length rapidly increased when shark reached a length of 63 to 76 cm and became stable at 73 cm length. All the sharks greater than 61 cm had rigid clasper while smaller ones had smooth clasper (Figure 8).

## Discussion

In the present study, the exponent b ranged between 2.5 and 3.5. Thus, the estimated parameters were acceptable (Froese, 2006).

We were able to obtain individuals across a full range of lengths for both sexes, although the sampled length structures of these sexes were very different

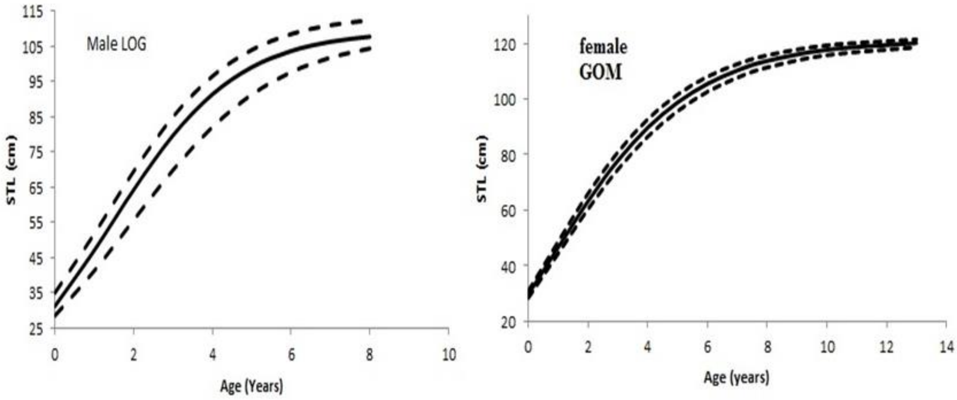

**Figure 5.** Length at age of *Carcharhinus dussumeiri* as determined from vertebral growth analysis.

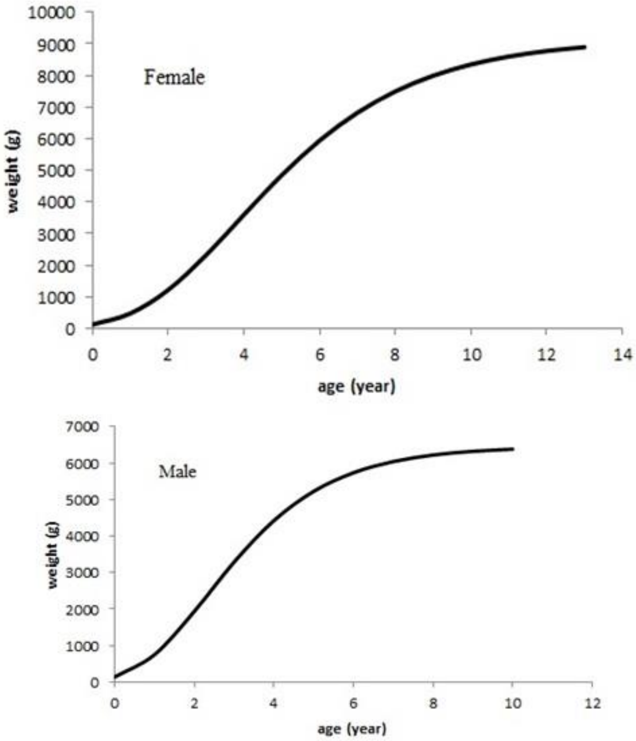

**Figure 6.** Fitted curves of weight-age relationship by the best parameters selected based on Akaike information criterion.

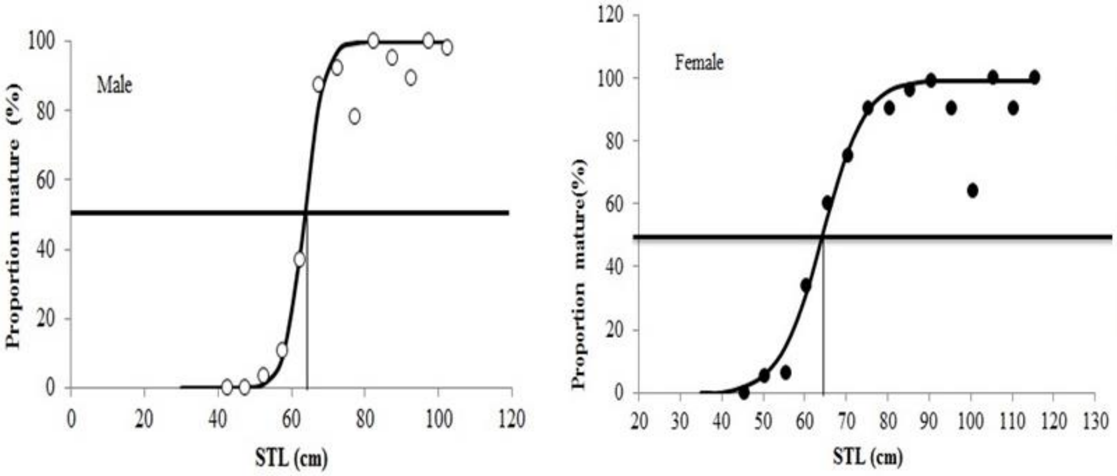

**Figure 7**. Mean length of male and female sharks at 50% maturity.

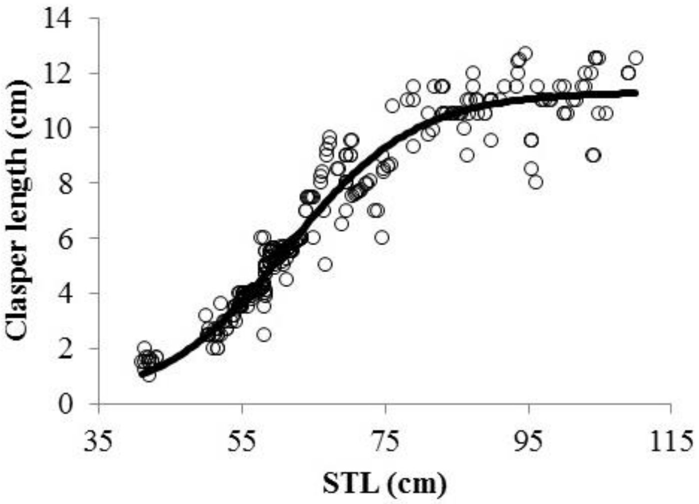

**Figure 8.** Relationship between clasper length and stretch total length in white cheek shark.

This bias toward juveniles in *C. dussumieri* probably explains why a distinct asymptote was not reached in any of the growth curve models, and consequently why $L_\infty$ exceeded the maximum length, specifically for males (males generally appear to grow to ~ 106 cm, whereas the fitted values of $L_\infty$ reached 120 cm in several models (Table 2).

The lack of an asymptote is of typical feature in many shark growth curves (Simpfendorfer *et al.*, 2002; Braccini *et al.*, 2007), and computer simulation studies have shown that it might be attributed to the selectivity of the fishing gear and the effects of length-selective fishing mortality (Walker *et al.*, 1998; Thorson and Simpfendorfer, 2009). If age underestimation has also occurred, probably this would further compound the issue.

Results of maturity stage from the current study detected that all the mature specimens had a hard and calcified clasper while immature ones showed a smooth clasper. Observations from similar studies on the reproductive biology of white cheek shark and the other species approved the results presented here (Asadi, 2001; Harry *et al.*, 2013; Henderson *et al.*, 2006).

A sigmoid relationship was found between clasper length and total length, indicating a slow growth rate in clasper length at earlier stages of life followed by a rapid rate during maturity stage and again a slow rate at post-maturity stage. Previous studies confirmed the sigmoid relationship between these parameters (Asadi, 2001; Harry, *et al.*, 2013, Henderson *et al.*, 2006, Capae, 1993).

. In a previous research on reproductive biology of white cheek shark by Asadi (2001), $Lm_{50}$ values for males and females was reported 68.9 and 68.7 cm, respectively, which exceeded than our estimates. When fishing pressure increases maturity at an earlier age and smaller size is sometimes a natural response in fish population (Rochet, 2000). Therefore, this can be justified by the increased fishing pressure in recent years.

Despite the fact sharks are commonly caught in countries along the borderline of the Persian Gulf and the Oman Sea, there is little information on their biology and, in many cases, and stocks are not well-known. In the Persian Gulf, sharks are considered as an important component of the commercial catch while a few studies have been conducted on its biology and reproduction. The present work can be applied as a basis for future studies.

## References

Aires-da-Silva, A. M. and Gallucci, V. F. 2007. Demographic and risk analyses applied to management and conservation of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. Marine and Freshwater Research, **58**: 570–580. doi:10.1071/MF06156

Asadi, M. 2001. Reproduction biology of *Carcharhinus dussumeiri* in Hormozgan waters. Iranian Journal of Fisheries Science, **1**: 1-18.(in Persian)

Braccini, J. M., Gillanders, B. M., Walker, T. I. and Tovar-Avila, J. 2007. Comparison of deterministic growth models fitted to length-at-age data of the piked spurdog (*Squalus megalops*) in south-eastern Australia. Marine and Freshwater Research, 58: 24–33. doi:10.1071/MF06064

Burnham, K. P. and Anderson, D. R. 2001. Kullback–Leibler information as a basis for strong inference in ecological studies. Wildlife Research, 28: 111–119. doi:10.1071/WR99107.

Cailliet, G. M. and Goldman, K. J. 2004. Age determination and validation in chondrichthyan fishes. In ‘Biology of sharks and their relatives’. (Eds JC Carrier, JA Musick and MR Heithaus.) pp. 399–448. (CRC Press: Boca Raton, FL.). 10.1201/9780203491317.pt3.

Capape, C. 1993. New data on the reproductive biology of the thorny stingray, *Dasyatis centroura* (Pisces, Dasyatidae) from off the Tunisian coasts. Environmental Biology of Fishes, 38: 73–80. doi:10.1007/BF00842905

Carpenter, K. E., Krupp, F., Jones, D. A. and Zajonz, U. 1997. FAO species identification guide for fishery purposes. The living marine resources of Kuwait, Eastern Saudi Arabia, Bahrain, Qatar, and the United Arab Emirates. FAO, Rome, ISBN 92-5-103741-8, 293 pp.

Chang, W.Y.B. 1982. A statistical-method for evaluating the reproducibility of age-determination. Canadian Journal of Fisheries and Aquatic Sciences, 39: 1208–1210. doi:10.1139/F82-158

Cortes, E. 1999. Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science, 56: 707–717.

Evans, G. T. and Hoenig, J. M. 1998. Testing and viewing symmetry in contingency tables, with application to readers of fish ages. International Biometrics Society, 54: 620–629. doi:10.2307/3109768

Fischer, W. and Bianchi, G. 1984. FAO species identification sheets for fishery purposes, Western Indian Ocean, Vols. 1-V, FAO, Rome, Italy.

Froese, R. 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. Journal of Applied Ichthyology, 22: 241–253. 10.1111/j.1439-0426.2006.00805.x

Gayanilo, F.C. and Pauly, D. 1997. Computed information series fisheries, FAO-ICLARM stock assessment tools. Reference manual. Rome Italy, 262 p.

Gelsleichter, J., Musick, J. A. and Nichols, S. 1999. Food habits of the smooth dogfish, *Mustelus canis*, dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, and the sand tiger, *Carcharias taurus*, from the northwest Atlantic Ocean. Environmental Biology of Fishes. 54: 205–217. doi:10.1577/1548 8659(1997)126,0862:UOCAAF.2.3.CO;2

Goldman, K. J. and Musick, J. A. 2006. Growth and maturity of salmon sharks (*Lamna ditropis*) in the eastern and western North Pacific, and comments on back-calculation methods. Fishery Bulletin, 104: 278–292.

Haddon, M. 2011. Modelling and quantitative methods in fisheries, 2nd edn. CRC Press, Taylor & Francis Group, New York, pp.449.

Harry, A.V, Andrew, J. and Simpfendorfer, C. A. 2013. Age, growth and reproductive biology of the spot-tail shark, *Carcharhinus sorrah*, and the Australian blacktip shark, *C. tilstoni*, from the Great Barrier Reef World Heritage Area, north-eastern Australia. Marine and freshwater research, 64: 277-293. doi:10.1071/MF12142

Henderson, A.C., Mcllwain, H.S., Al-Cufi, J.L. and Ambu-Ali, A. 2006. Reproductive biology of the milk shark Rhizoprionodon acutus and the bigeye houndshark Iago omanensis in the coastal waters of Oman. Journal of fish biology, 68: 1662-1678. Doi:10.1002/aqc.2635.

Institutional Web Pages: Shark research committee, 2015. Information about save the shark. http://Sharkresearchcommittee.com (accessed January 12, 2015).

Katsanevakis, S. and Maravelias, C. D. 2008. Modelling fish growth: multi-model inference as a better alternative to a priori using von Bertalanffy equation. Fish and Fisheries, 9: 178–187. doi:10.1111/J.1467-2979.2008.00279.X

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P. and Peterson, C. H. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science, 315: 1846-1850. 10.1126/science.1138657

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. ICES Journal of Marine Sciencee. 39(2): 175-192. 10.1093/icesjms/39.2.175

Punt, A. E., Pribac, F., Walker, T. I., Taylor, B. L. and Prince, J. D. 2000. Stock assessment of school shark, *Galeorhinus galeus*, based on a spatially explicit population dynamics model. Marine and Freshwater Research, 51: 205–220. doi:10.1071/MF99124

Roa, R; Ernst, B. and Tapia, F. 1999. Estimation of size at sexual maturity: an evaluation of analytical and re-sampling procedures. Fishery Bulletin, **97**: 570–580.

Rochet, M. J. 2000. May life history traits be used as indices of population viability? Journal of Sea Research, **44**: 145–157. doi:10.1016/S1385-1101(00)00041-1

Simpfendorfer, C. A., McAuley, R. B., Chidlow, J. and Unsworth, P. 2002. Validated age and growth of the dusky shark, Carcharhinus obscurus, from Western Australian waters. Marine and Freshwater Research: 53: 567–573. doi:10.1071/MF01131

Stevens, J. D., Bonfil, R., Dulvy, N. K. and Walker, P. A. 2000. The effects of fishing on sharks, rays, and chimaeras (Chrondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science, 57: 476–494. doi:10.1071/MF98158

Thorson, J. T., Simpfendorfer, C. A. 2009. Gear selectivity and sample size effects on growth curve selection in shark age and growth studies. Fisheries Research, 98: 75–84. doi:10.1016/J.FISHRES.2009.03.016

Walker, T. I. 2005. Reproduction in fisheries science. In ‘Reproductive Biology and Phylogeny of Chondrichthyans: Sharks, Batoids, and Chimaeras’. (Ed. W. C. Hamlett.) pp. 81–127. (Science Publishers: Enfield, NH.)

Walker, T. I., Taylor, B. L., Hudson, R. J. and Cottier, J. P. 1998. The phenomenon of apparent change of growth rate in gummy shark (*Mustelus antarcticus*) harvested off southern Australia. Fisheries Research, 39: 139–163. doi:10.1111/J.1095-8649.2010.02654.X

Ward, p. and Myers, R.A. 2005. Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology, 86(4): 835-847. 10.1890/03-0746.