



Stock Assessment of Two Parrotfish, *Hipposcarus harid* and *Scarus ferrugineus* in Jeddah, Saudi Arabia

Ahmad Osman Mal¹ and Mohamed Hosny Gabr^{1,2,*}

¹Marine Biology Department, Faculty of Marine Science, King Abdulaziz University, P.O. Box 80207, Jeddah 21589 Saudi Arabia

²National Institute of Oceanography and Fisheries, Suez, Egypt

ABSTRACT

The current stock status of two Parrotfish, *Hipposcarus harid* and *Scarus ferrugineus* in Jeddah was assessed. Scales were used for age determination and back calculations of length-at-ages. The growth parameters were estimated to be: the asymptotic length $L_{\infty} = 54.044$ cm, the growth coefficient $K = 0.168$ year⁻¹, and age at zero length $t_0 = -0.707$ year for *H. harid* and $L_{\infty} = 51.238$ cm, $K = 0.170$ year⁻¹, and $t_0 = -0.889$ year for *S. ferrugineus*. The total 'Z', natural 'M', fishing 'F' mortality coefficients and current exploitation 'E_{cur}' were 0.96, 0.294, 0.670 year⁻¹, and 0.69 year⁻¹, respectively for *H. harid* and 0.77, 0.299, 0.471 year⁻¹, and 0.61 year⁻¹ respectively for *S. ferrugineus*. The maximum yield per recruit at the current fishing mortality was 108.1 g for *H. harid* and 137.6 g for *S. ferrugineus*. The biological reference points: $F_{max} = 0.401$ year⁻¹ and $F_{0.1} = 0.245$ year⁻¹ for *H. harid* and $F_{max} = 0.434$ year⁻¹ and $F_{0.1} = 0.307$ year⁻¹ for *S. ferrugineus* were lower than the current fishing mortality, reflecting an over-exploitation for both species. The current fishing mortality is recommended to be decreased to the target reference point $F_{0.1} = 0.453$ year⁻¹ for *H. harid* and $F_{0.1} = 0.466$ year⁻¹ for *S. ferrugineus* after increasing the age at first capture to be 3 years for both species.

Article Information

Received 29 July 2017

Revised 12 May 2018

Accepted 06 August 2019

Available online 09 December 2019

Authors' Contribution

AOM and MHG initiated and designed the study and collected the samples. MHG conducted the experiments and wrote the article. AOM reviewed the article.

Key words

Hipposcarus harid, *Scarus ferrugineus*, Age determination, Growth parameters, Mortality coefficients, Maximum yield per recruit.

INTRODUCTION

Hipposcarus harid (Forsskål, 1775) and *Scarus ferrugineus* (Forsskål, 1775) are two species of Parrotfishes. Ongoing phylogenetic and evolutionary research on parrotfishes indicate that they are either a separate family (Scaridae) under the suborder Labroidae (Bellwood, 1994; Randal, 2007) or a subfamily (Scarinae) under the family Labridae (Westneat and Alfaro, 2005). Parrotfishes are a dominant group of herbivorous species that play an important role in bioerosion and hence affect the benthic communities' structure on coral reefs (Williams and Hatcher 1983; Russ, 1984; Choat and Bellwood, 1991; Alwany *et al.*, 2009).

Parrotfishes are also important fishery resources in coral reef small-scale artisanal fisheries and caught mainly in gillnet and pot fishing gears. As indicated by Lokrantz *et al.* (2008), the decline in the biomass and abundance of parrotfishes due to overfishing may have severe negative impacts on the coral reefs dynamics and regeneration. In Saudi Arabia, parrotfishes represent an important part of the catch of coral reef fisheries which are abundant along the Red Sea coast. The average annual catch of parrotfishes

from the Red Sea coast of Saudi Arabia during the period from 2008–2016 was 364 tones (FAO, 2018). The two parrotfish species *Hipposcarus harid* and *Scarus ferrugineus* are a major component of parrotfish catch from Jeddah fisheries.

The growth rates and longevity in some scarid species have been reported in previous studies based on alternating light and dark bands in hard structures (Warner and Downs, 1977; Russ and St. John, 1988; Clifton, 1995; van Rooij *et al.*, 1995). However, there are only a few studies on the age and growth of the two species in the Red Sea (Ali *et al.*, 2011; Mehanna *et al.*, 2014). There are no previous studies available on the stock assessment for these two parrotfish species in Jeddah fisheries.

The aim of the present study was to estimate age and growth using scales as hard structures, mortalities, length and age at first capture, yield and biomass per recruit of the two parrotfish species in Jeddah fisheries.

MATERIALS AND METHODS

Representative samples of the two parrotfish species *Hipposcarus harid* and *Scarus ferrugineus* were collected monthly from the daily fish auction held at the main fish landing site of Jeddah (main fish market) during the period from March 2013 to January 2014. Samples were collected randomly from the landed catch which is harvested using

* Corresponding author: mhosnyg@yahoo.com
0030-9923/2020/0001-0001 \$ 9.00/0

Copyright 2020 Zoological Society of Pakistan

the different fishing gears in Jeddah (Fig. 1), to minimize biases in the sample size distributions produced by differences in gear selectivity (Goodyear, 1995).



Fig. 1. Map showing Jeddah fisheries in the Red Sea.

For each specimen, the total fish length (L) was measured to the nearest 0.1 cm and total body weight (W) was recorded to the nearest 0.1 g. The power equation: $W = a L^b$ was used to describe the length-weight relationship, where a is the intercept and b is the slope estimated from the linear regression analysis of the following linearized form of the power equation:

$$\ln W = \ln a + b \ln L$$

For age determination, scales from behind the left pectoral fin were collected, cleaned in water then dried and mounted between two microscopic glass slides. The mounted scales were examined under a stereo-zoom microscope (MEIJI) using a digital video camera connected to a personal computer, where Micrometrics SE Premium software was used to capture and save pictures for scale measurements.

Two linear regression analyses were used to describe the relationship between the body length (L) and scale radius (S) for the two species. The first one is the regression

of L on S based on the linear form: $L = c + d S$ (c is the intercept, d is the slope), and the second is the regression of S on L based on the linear form: $S = e + f L$ (e is the intercept, f is the slope). The Lengths corresponding to previous years of life were estimated (back-calculated) using three back-calculation methods (Francis, 1990; Pierce *et al.*, 1996):

Fraser-Lee equation (Lee, 1920):

$$L_i = c + (L - c) (S_i / S)$$

Body proportional hypothesis (BPH):

$$L_i = [(c + d S_i) / (c + d S)] L$$

Scale proportional hypothesis (SPH):

$$L_i = -(e/f) + [L + (e/f)] (S_i / S)$$

Where, L is the observed (at capture) fish length, S is the scale radius (at capture), L_i is the back-calculated length at the time of annulus i formation, S_i is the radius of the annulus i . The mean calculated lengths at ages estimated by the three methods were compared using a one-way analysis of variance (ANOVA) test, applied using 'Statistix 8.1' software (Analytical Software, Tallahassee, USA).

The asymptotic length (L_∞) and growth coefficient (K) are two parameters of the von Bertalanffy (1938) growth equation (VBGE): $L_t = L_\infty [1 - e^{-K(t-t_0)}]$. Both parameters were estimated using the method of Ford (1933) and Walford (1946) fitted to the average back-calculated lengths-at-ages. The third growth parameter (t_0) (supposed age at zero length) was estimated, based on the estimated values of L_∞ and K , by re-arranging the von Bertalanffy growth equation as described by Sparre and venema (1998): $t_0 = t + 1/K \log_e (1 - L_t / L_\infty)$.

The performance index of growth in length ' ϕ' ' for both species was calculated by the formula suggested by Pauly and Munro (1984): $\phi' = \log K + 2 \log L_\infty$ and applied in recently published papers (Ceyhan *et al.*, 2019). Because this index is based on length which is rarely lost by fish, it is considered the most precise and flexible index of growth performance which can be used to compare growth performances of wild and cultured fish stocks (Mathews and Samuel, 1990).

The linearized length-converted catch curve method of Pauly (1983), implemented in the FiSAT II software (Gayaniilo *et al.*, 2005), was used to estimate the instantaneous total mortality coefficient ' Z '. The natural mortality coefficient ' M ' was estimated by the equation proposed by Jensen (1996) and modified by Hamel (2015) as follows: $M = 1.753 K$, where K is the growth coefficient. The difference between the total mortality coefficient ' Z ' and the natural mortality coefficient ' M ' was accounted to the fishing mortality coefficient ' F '. The exploitation ratio ' E ' was expressed by the ratio between F and Z ($E = F/Z$).

Three types of fishing gears; gillnets, trammel nets

and fish pots are working on all sizes in the fish populations of *H. harid* and *S. ferrugineus* in Jeddah fisheries. Based on Crone *et al.* (2013), since the selectivity of at least one gear type; fish pots, is considered to be sigmoidal (similar to the trawl codend selectivity) (Stewart and Ferrell, 2001; Boutson *et al.*, 2009; Songrak *et al.*, 2013), it is assumed, in the present study, that the gear selectivity for *H. harid* and *S. ferrugineus* is asymptotic (sigmoidal) and thus the length at first capture ' L_c ' (the mean selection length at which 50% of the fish that entered the fishing gear are retained) for both species was estimated using the cumulative method described by Pauly (1984b) implemented in the FiSAT II software. The age ' t_c ' corresponding to L_c was estimated by applying the inverse von bertalanffy equation as follows: $t_c = t_0 - 1/K \text{Log}_e(1 - L_c / L_\infty)$.

The model of Beverton and Holt (1957) was used to estimate the yield per recruit Y/R and biomass per recruit B/R of *H. harid* and *S. ferrugineus* in Jeddah fisheries as follows:

$$\frac{Y}{R} = F \times \text{Exp} [-M \times (t_c - t_r)] \times W_\infty \times \left[\frac{1}{Z} - \left(\frac{3S}{Z+K} \right) + \left(\frac{3S^2}{Z+2K} \right) - \left(\frac{S^3}{Z+3K} \right) \right]$$

Where, Y/R is yield per recruit, F is the fishing mortality coefficient, M is the natural mortality coefficient, t_c is the mean age at first capture, t_r is the mean age at recruitment, W_∞ is the asymptotic weight, Z is total mortality coefficient, K is the growth coefficient and S equal to the equation: $S = e^{-K(t_c - t_0)}$. The biomass per recruit (B/R) was estimated by dividing the Y/R by the fishing mortality F .

Two yield-based biological reference points were determined at two levels of length at first capture L_c : $F_{\max}$ (the fishing mortality level that produces the maximum yield per recruit) and $F_{0.1}$ (the fishing mortality level at which the slope or marginal increment of the yield per recruit is 10% of its value at the origin, where $E=0$). The current fishing mortality level F_{cur} was matched with these reference

points. $F_{\max}$ is referred to as the 'Limit' reference point, while $F_{0.1}$ is considered as the target reference point (Gabriel and Mace, 1999; Cadima, 2003; Hoggarth *et al.*, 2006).

RESULTS

Fishing gears

Scarid species, as herbivores, are usually caught with gillnets, trammel nets and fish traps (pots). Table I shows the specifications of gillnets and trammel nets used to catch most of the parrotfishes landed in Jeddah fisheries. Two fishermen on a wooden boat (7–9 m length) provided with outboard engine of 25–40 HP usually use some units of gillnets to set in the lagoons and trammel nets to set on the reef flat (mainly during daytime) to target parrotfishes among other reef fishes in the coral reef fisheries of Jeddah.

Age determination and back-calculations

By counting the number of annuli that appeared on the scales, the age in years could be assigned to each specimen. Twelve age groups (0-11) could be determined for *H. harid* based on scales reading of 667 specimens ranging from 12.4 – 48.2 cm in total length, while fifteen age groups (0-14) were observed for *S. ferrugineus* based on 516 specimens ranging in total length from 13.2–48.5 cm.

The relationship between the fish length and scale radius was found to be linear, as shown in Figure 2, and the model of linear regression of L on S was the best fit for this relationship where the regression standardized residuals plotted against predicted lengths showed no clear pattern but random scattering around zero line (Fig. 2). For back-calculations, the fish length - scale radius relationship could be described by the following two linear equations for each species, based on the linear regression analysis for pooled data (sexes combined):

Table I.- Specifications of gillnets and trammel nets used in Jeddah coral reef fisheries.

Gear Item	Gillnets	Trammel nets
Unit length	35 - 40 m	45 - 50 m
Net depth	1.0 - 1.2 m	0.9 - 1 m
Number of Units per boat	4 - 6	6 - 8
Float line material and diameter	Polyethylene, 5 - 6 mm	Polyethylene, 4 - 5 mm
Lead line material and diameter	Polyethylene, 4 - 5 mm	Polyethylene, 4 - 5 mm
Number and material of floats per unit	45-50 Cork floats, 25 gf	60-70 Cork floats, 25 gf
Distance between two floats	85 - 90 cm	60 - 65 cm
Number of lead sinkers per unit	70 - 75 (30 g each)	110 - 120 (35 g each)
Distance between two sinkers	65 - 70 cm	35 - 40 cm
Inner panel mesh size and twine diameter	62 - 88 mm; 0.3-0.4 mm	50 - 62 mm; 0.3 mm
Outer panel mesh size and twine diameter	Not present	150 - 170 mm; 0.4 mm
Twine material	Polyamide, Mono- or Multi-filament	Polyamide, monofilament

Table II.- The mean back-calculated lengths at ages estimated by three methods: Fraser -Lee, Body proportional hypothesis (BPH) and Scale proportional hypothesis (SPH) for *H. harid* and *S. ferrugineus* collected from Jeddah fisheries.

Age	<i>H. harid</i>					<i>S. ferrugineus</i>				
	Fraser-Lee (pooled)	Females	Males	Pooled	SPH (pooled)	Fraser-Lee (pooled)	Females	Males	Pooled	SPH (pooled)
1	13.83	14.26	14.58	13.82	12.90	14.59	14.81	14.54	14.59	13.89
2	20.72	20.82	21.20	20.71	20.36	21.09	21.37	20.97	21.09	20.71
3	25.80	25.82	25.65	25.79	25.52	25.81	25.29	26.10	25.81	25.55
4	29.72	29.34	29.73	29.71	29.39	29.22	29.16	29.27	29.21	28.93
5	32.98	32.80	33.24	32.97	32.66	32.21	32.80	32.18	32.21	31.89
6	35.84	-	35.96	35.83	35.38	35.24	36.42	35.11	35.24	35.01
7	38.50	-	38.60	38.49	38.09	37.45	38.65	37.9	37.44	37.15
8	41.13	-	41.20	41.12	40.87	39.39	40.30	39.11	39.38	39.17
9	43.53	-	43.57	43.52	43.36	41.16	41.73	41.00	41.16	41.02
10	45.30	-	45.34	45.29	45.14	42.79	-	42.80	42.78	42.68
11	46.78	-	46.79	46.77	46.70	44.30	-	44.30	44.29	44.24
12	-	-	-	-	-	45.58	-	45.59	45.58	45.47
13	-	-	-	-	-	46.69	-	46.70	46.69	46.62
14	-	-	-	-	-	47.60	-	47.60	47.59	47.56

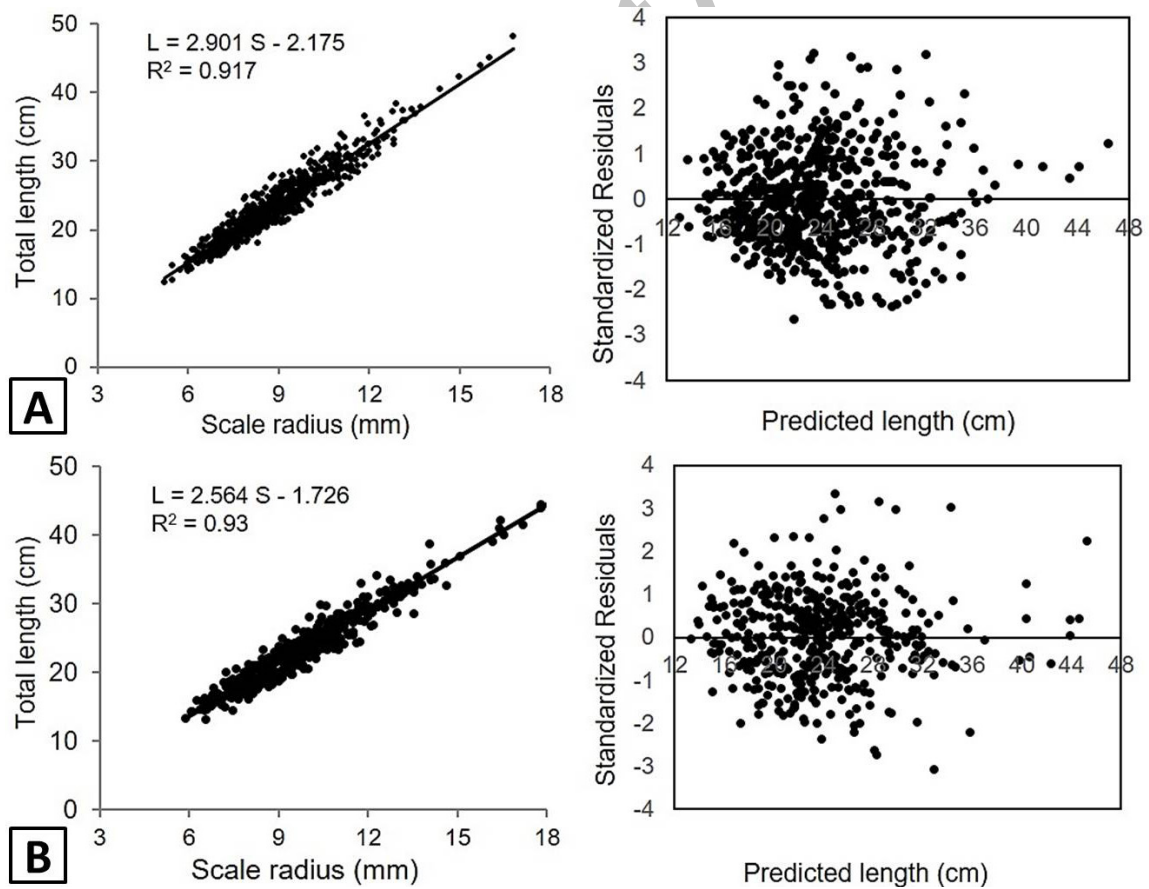


Fig. 2. Total length-otolith radius relationship and the residuals plot of *H. harid* (A) and *S. ferrugineus* (B) collected from Jeddah fisheries.

For *H. harid* ($R^2 = 0.917$):

$$L = 2.901 S - 2.175 \text{ (regression of L on S)}$$

$$S = 1.549 + 0.316 L \text{ (regression of S on L)}$$

For *S. ferrugineus* ($R^2 = 0.930$):

$$L = 2.564 S - 1.726 \text{ (regression of L on S)}$$

$$S = 1.321 + 0.363 L \text{ (regression of S on L)}$$

The results listed in Table II and represented in Figure 3 show the mean of the individual back-calculated lengths at ages that estimated by the three back-calculation formulae used in this study. Results of the ANOVA test indicated that there is no statistically significant difference between the mean lengths at ages that estimated by the three back-calculation methods for *H. harid* ($F=0.0034$, $P=0.9966$) and *S. ferrugineus* ($F=0.0023$, $P=0.9977$).

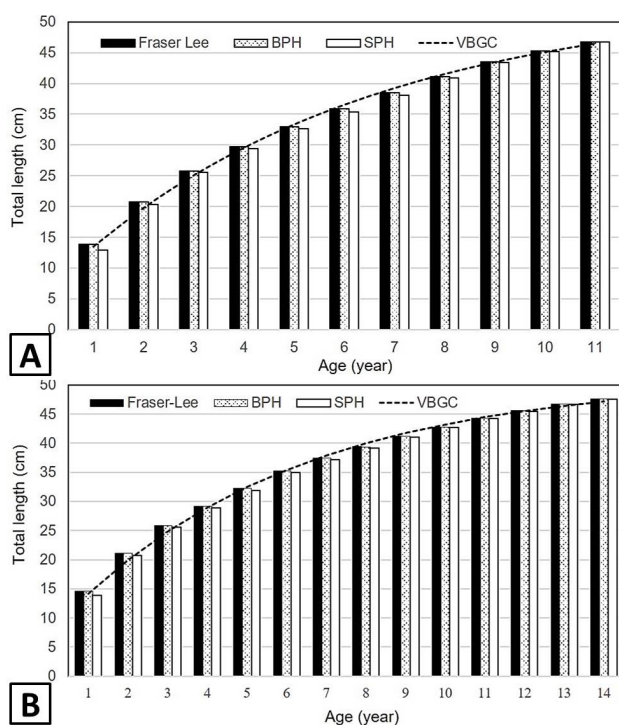


Fig. 3. Mean back-calculated lengths at ages (estimated by three different methods) and von Bertalanffy growth curve for *H. harid* (A) and *S. ferrugineus* (B).

The mean calculated lengths at corresponding ages that estimated by the body proportional hypothesis (BPH) formula for males and females for each species (listed in Table II) were found to be not statistically significantly different (*H. harid*: $F=0.003$, $P=0.954$; *S. ferrugineus*: $F=0.02$, $P=0.894$). So, the growth in length and annual increment were determined from the mean calculated lengths at ages that estimated by the body proportional hypothesis (BPH) formula applied on pooled data (sexes combined) for each species and the results are represented

in Figure 4.

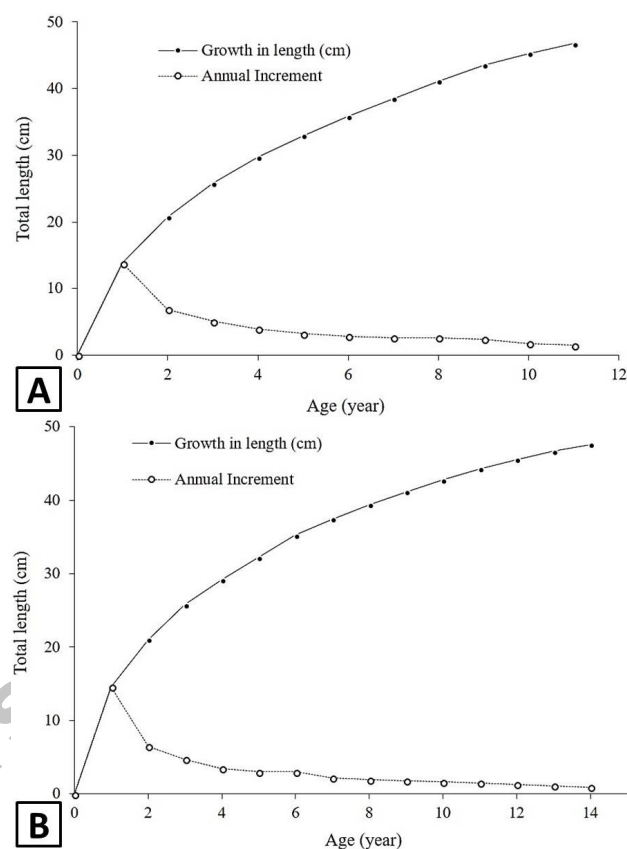


Fig. 4. Growth in length and annual increment of *H. harid* (A) and *S. ferrugineus* (B) collected from Jeddah fisheries.

The growth equation

Applying the Ford (1933) and Walford (1946) method to the mean lengths at ages estimated by the body proportional hypothesis (BPH) formula applied on pooled data, the growth parameters; L_{∞} , K could be estimated and then the value of t_0 was determined and thus the VBGE for describing the growth in length of both species could be written as follows: $L_t = 54.0436 [1 - e^{-0.168(t+0.707)}]$ for *H. harid* and $L_t = 51.238 [1 - e^{-0.170(t+0.889)}]$ for *S. ferrugineus*. The von bertalanffy growth curves are shown in Figure 5.

Length-weight relationship and growth in weight

Total fish lengths and their corresponding weights for *H. harid* and *S. ferrugineus* are represented in Figure 6. The length - weight relationship for both species could be described by the nonlinear (power) equations as follows: For *H. harid*:

$$W = 0.026 L^{2.81} (R^2 = 0.967, n = 73 \text{ males})$$

$$W = 0.021 L^{2.91} (R^2 = 0.986, n = 594 \text{ females})$$

$$W = 0.027 L^{2.82} (R^2 = 0.985, n = 667 \text{ both sexes})$$

For *S. ferrugineus*:

$$W = 0.020 L^{2.973} \quad (R^2 = 0.987, n = 221 \text{ males})$$

$$W = 0.017 L^{3.036} \quad (R^2 = 0.985, n = 295 \text{ females})$$

$$W = 0.020 L^{2.970} \quad (R^2 = 0.989, n = 516 \text{ both sexes})$$

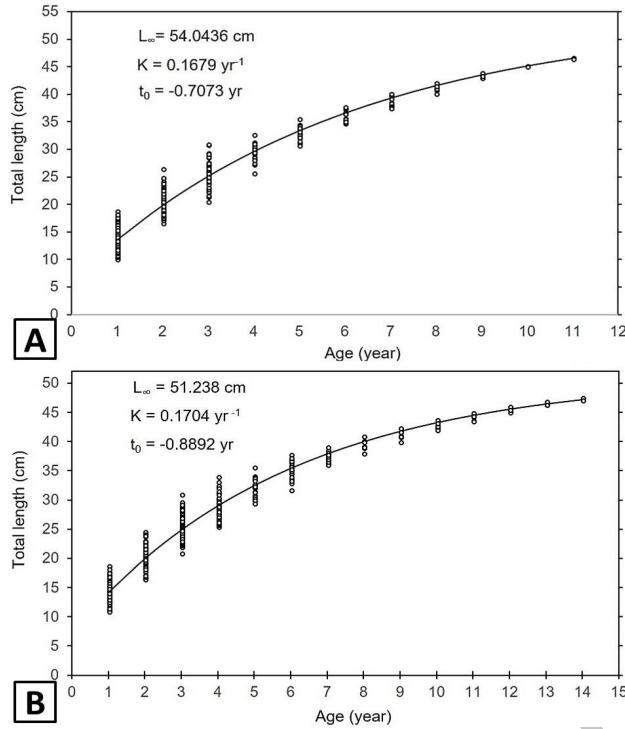


Fig. 5. von Bertalanffy growth curve for *H. harid* (A) and *S. ferrugineus* (B) collected from Jeddah fisheries.

To check if the growth is isometric (having the value of the exponent 'b' equal to 3) or not, the estimated value of 'b' for males and females was tested if it was significantly different from 3 or not using the t-test of Pauly (1984a). The results of the t-test indicated that the growth of males and females of *H. harid* is negatively allometric where the 'b' values for both males and females are significantly smaller than the slope value '3' of the isometric growth (for males: $t = 3.0852$, critical t value = 1.994 for $P = 0.05$; for females: $t = 6.3257$, critical t value = 1.965 for $P = 0.05$). For *S. ferrugineus*, the growth of males and females was revealed to be isometric, where the b values were found to be not significantly different from the slope '3' of the cubic law of the isometric growth (for males: $t = 1.171$, critical t value = 1.972 for $P = 0.05$; for females: $t = 1.6449$, critical t value = 1.972 for $P = 0.05$).

Using the obtained equations describing the length-weight relationship for both species, the back-calculated lengths at ages were used to estimate their corresponding weights at ages and thus calculate the growth in weight for both species shown in Figure 7.

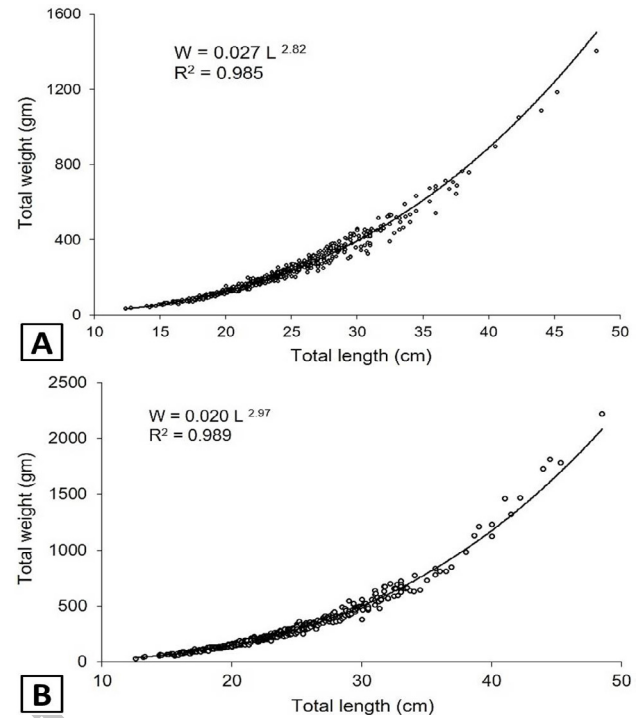


Fig. 6. Length-weight relationship of *H. harid* (A) and *S. ferrugineus* (B) collected from Jeddah fisheries.

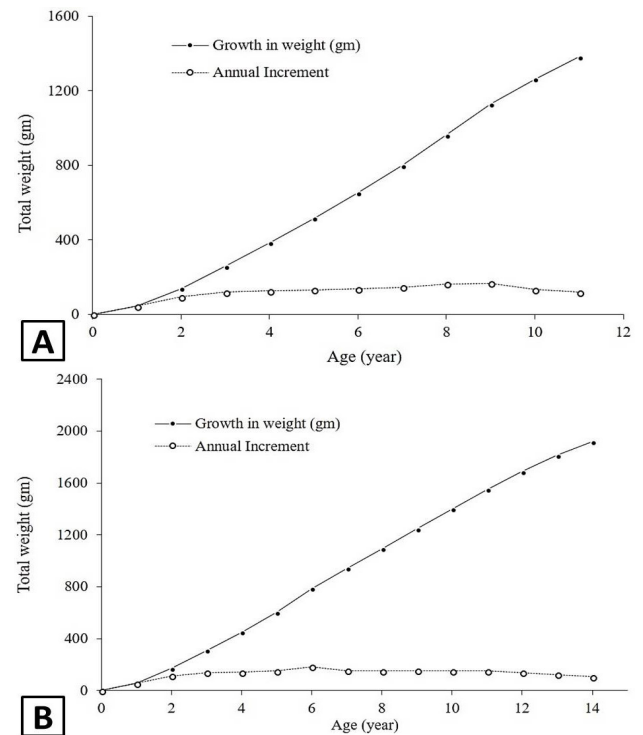


Fig. 7. Growth in weight and annual increment of *H. harid* (A) and *S. ferrugineus* (B) collected from Jeddah fisheries.

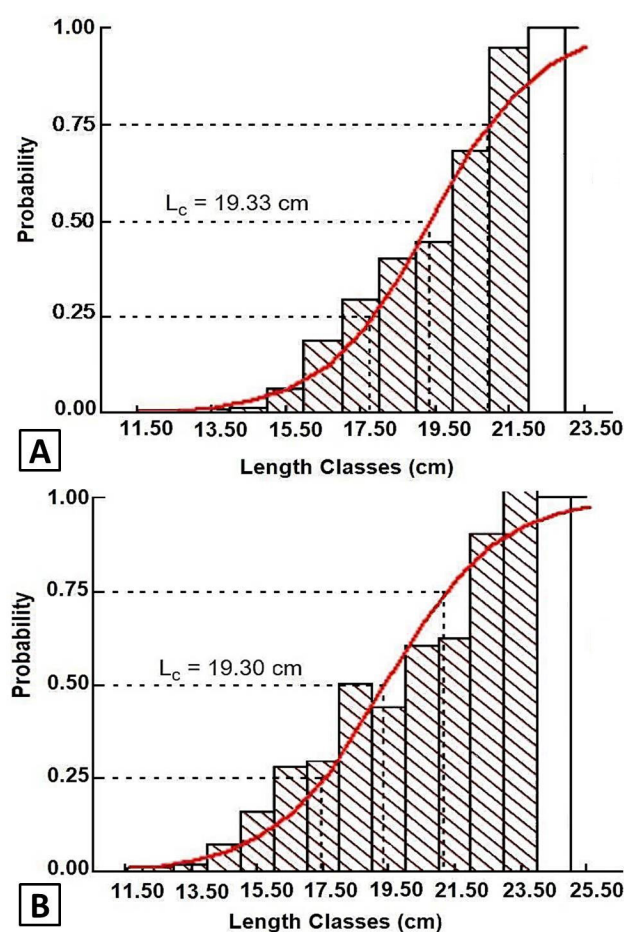


Fig. 8. Length at first capture L_c of *H. harid* (A) and *S. ferrugineus* (B) collected from Jeddah fisheries.

Length and age at first capture

Figure 8 shows the results concerning the probability of capture of both species *H. harid* (A) and *S. ferrugineus* (B) obtained by the cumulative method described by Pauly (1984b) in the FiSAT II software. The length at 50% probability of capture $L_{50\%}$ or L_c and its corresponding age t_c was found to be 19.33 cm and 1.93 year for *H. harid* and 19.30 cm and 1.88 year for *S. ferrugineus*.

Mortalities and current exploitation

The instantaneous total mortality coefficient Z for *H. harid* and *S. ferrugineus* was estimated as the absolute value of the slope of the right-hand descending line in Figure 9 (the linearized length-converted catch curve as obtained from the FiSAT II software). The value of Z was found to be 0.96 year⁻¹ for *H. harid* and 0.77 year⁻¹ for *S. ferrugineus*. The value of the natural mortality coefficient “ M ” was estimated as 0.294 year⁻¹ for *H. harid* and 0.299 year⁻¹ for *S. ferrugineus*. The fishing mortality coefficient

F was estimated to be 0.670 year⁻¹ for *H. harid* and 0.471 year⁻¹ for *S. ferrugineus*. The current exploitation rate E_{cur} , which is expressed as the ratio of F/Z , was determined to be 0.69 year⁻¹ for *H. harid* and 0.61 year⁻¹ for *S. ferrugineus*.

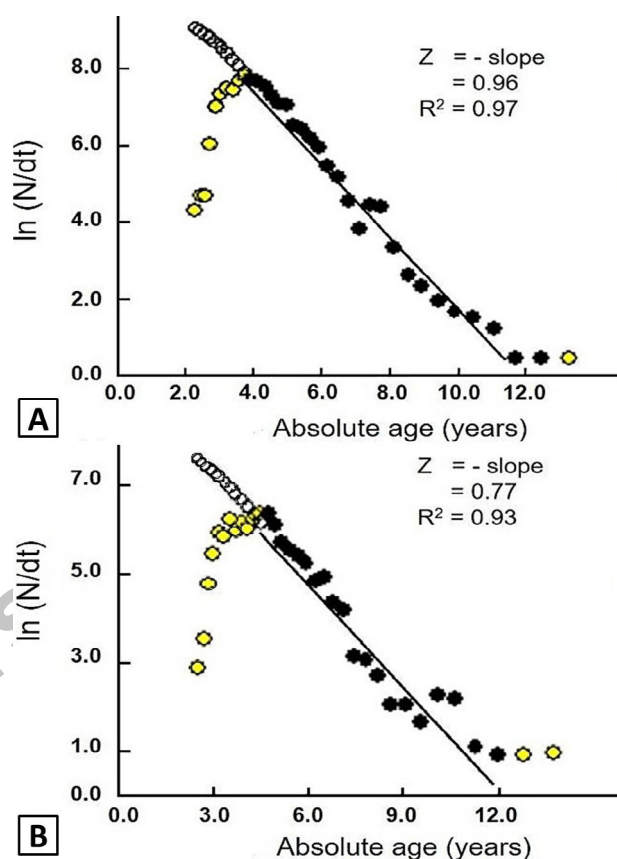


Fig. 9. Linearized Length-converted catch curve of *H. harid* (A) and *S. ferrugineus* (B) collected from Jeddah fisheries (closed circles represent the data points used in the regression analysis).

Table III.- Parameters used to estimate the yield per recruit of *H. harid* and *S. ferrugineus* collected from Jeddah fisheries.

Parameter	<i>H. harid</i>	<i>S. ferrugineus</i>
K	0.168 year ⁻¹	0.170 year ⁻¹
W_{∞}	2078.3 g	2390.7 g
t_0	-0.7073 year	-0.8894 year
t_c	1.93 year	1.88 year
t_e	2.99 year	3.04 year
t_r	0.85 year	0.77 year
M	0.294 year ⁻¹	0.299 year ⁻¹
Z	0.96 year ⁻¹	0.77 year ⁻¹
F_{cur}	0.67 year ⁻¹	0.471 year ⁻¹
F	Variable	Variable

Table IV.- The yield per recruit (Y/R) and biomass per recruit (B/R) corresponding to F_{cur} , $F_{0.1}$ and F_{max} at two values of age at first capture of *H. harid* and *S. ferrugineus* in Jeddah fisheries.

Reference point	<i>H. harid</i>						<i>S. ferrugineus</i>					
	$t_c = 1.93$ year			$t_c = 2.99$ year			$t_c = 1.88$ year			$t_c = 3.04$ year		
	F (year ⁻¹)	Y/R (g)	B/R (g)	F (year ⁻¹)	Y/R (g)	B/R (g)	F (year ⁻¹)	Y/R (g)	B/R (g)	F (year ⁻¹)	Y/R (g)	B/R (g)
$F_{0.1}$	0.245	107.6	439.0	0.453	126.7	279.7	0.307	134.7	438.6	0.466	153.4	329.1
F_{max}	0.401	112.5	280.6	0.686	129.0	188.0	0.434	137.7	317.2	0.830	158.1	190.4
F_{cur}	0.670	108.1	161.4	0.670	129.0	192.5	0.471	137.6	292.1	0.471	153.6	326.0

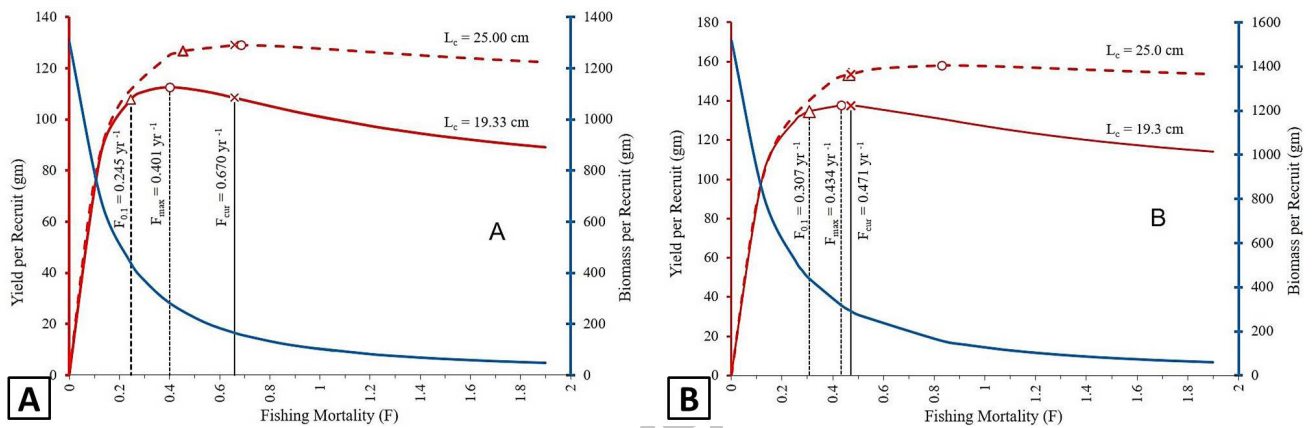


Fig. 10. Yield (red lines) and biomass (blue line) per recruit of *H. harid* (A) and *S. ferrugineus* (B) collected from Jeddah fisheries.

Maximum yield and biomass per recruit

The parameters used to estimate the yield per recruit of *H. harid* and *S. ferrugineus* in Jeddah fisheries are given in Table III. The estimated Y/R and B/R as a function of fishing mortality at two values of age at first capture $t_c = 1.93$ and 2.99 year for *H. harid* and $t_c = 1.88$ and 3.04 year for *S. ferrugineus* are shown in Figure 10.

The yield per recruit and biomass per recruit (in grams) corresponding to the current fishing mortality F_{cur} relative to those corresponding to the two biological reference points F_{max} and $F_{0.1}$ estimated at the two levels of age at first capture are listed in Table IV. For *H. harid*, at the current level of fishing mortality $F_{cur} = 0.67$ year⁻¹ and age at first capture $t_c = 1.93$ year, the yield and biomass per recruit were estimated to be 108.1 and 161.4 g, respectively. For *S. ferrugineus*, the current level of fishing mortality $F_{cur} = 0.471$ year⁻¹ and age at first capture $t_c = 1.88$ year, resulted in a yield per recruit of 137.6 g and a biomass per recruit of 292.1 g.

Increasing the age at first capture from 1.93 to 2.99 year (corresponding to 25 cm total length) for *H. harid* increased the yield and biomass per recruit at the current level of fishing mortality to 129.0 and 192.5 g, respectively. Similarly, when the age at first capture increased from 1.88 to 3.04 year (corresponding to 25 cm total length) for *S.*

ferrugineus, the yield and biomass per recruit at the current level of fishing mortality increased to 153.6 and 326.0 g, respectively.

DISCUSSION

Age determination and back-calculations

In the present study, the scales were used for age determination of *H. harid* and *S. ferrugineus* in Jeddah fisheries based on two criteria (Williams and Bedford, 1974): the recognized characteristic pattern shown on the scales (e.g., Fig. 11) and the annual time scale assigned for each pair of alternative opaque and hyaline bands (annulus) as confirmed in previous studies on scarid species (Warner and Downs, 1977; Lou, 1992; Fowler, 1995; Choat *et al.*, 1996; Ali *et al.*, 2011; Mehanna *et al.*, 2014).

In the present study, the relationship between fish length and scale radius showed that the larger the observed fish length (L), the larger the scale radius at capture (S), based on the strong linear relationship: $L = 2.901 S - 2.175$ for *H. harid* and $L = 2.564 S - 1.726$ for *S. ferrugineus*. For *H. harid* ranging in total length from 12.4 to 48.2 cm, eleven annuli were laid down on the scales, while for *S. ferrugineus* ranging in total length from 13.2 to 48.5 cm, fourteen annuli could be observed on the scales.

The back-calculated lengths at ages that are estimated by the Fraser-Lee formula and the body proportional hypothesis (BPH) formula were almost the same for both species. This is because the two methods were based on the same linear regression (L on S), whereas the scale proportional hypothesis (SPH) formula produced slightly lower back-calculated lengths at ages because it is based on a different linear regression (S on L) as indicated by Francis (1990). However, results of the ANOVA test showed that the difference between the back-calculated lengths at ages estimated by the three different methods for the two species (pooled data) was not statistically significant. These results agree well with what is reported by Pierce *et al.* (1996).

The back-calculated lengths at ages that are estimated by the body proportional hypothesis (BPH) formula, as one of the two proportional hypotheses recommended by Francis (1990) for back-calculations, were considered in the present study to calculate the growth in length and growth parameters for sexes combined (pooled data) since there was no statistically significant difference between the back-calculated lengths at corresponding ages for males and females. Because the two scarid species are protogynous (females change to males in case of deficiency) (Ali *et al.*, 2011; Choat and Robertson, 1975), females predominate in the younger length or age groups while being missed in older groups which are predominated by males.

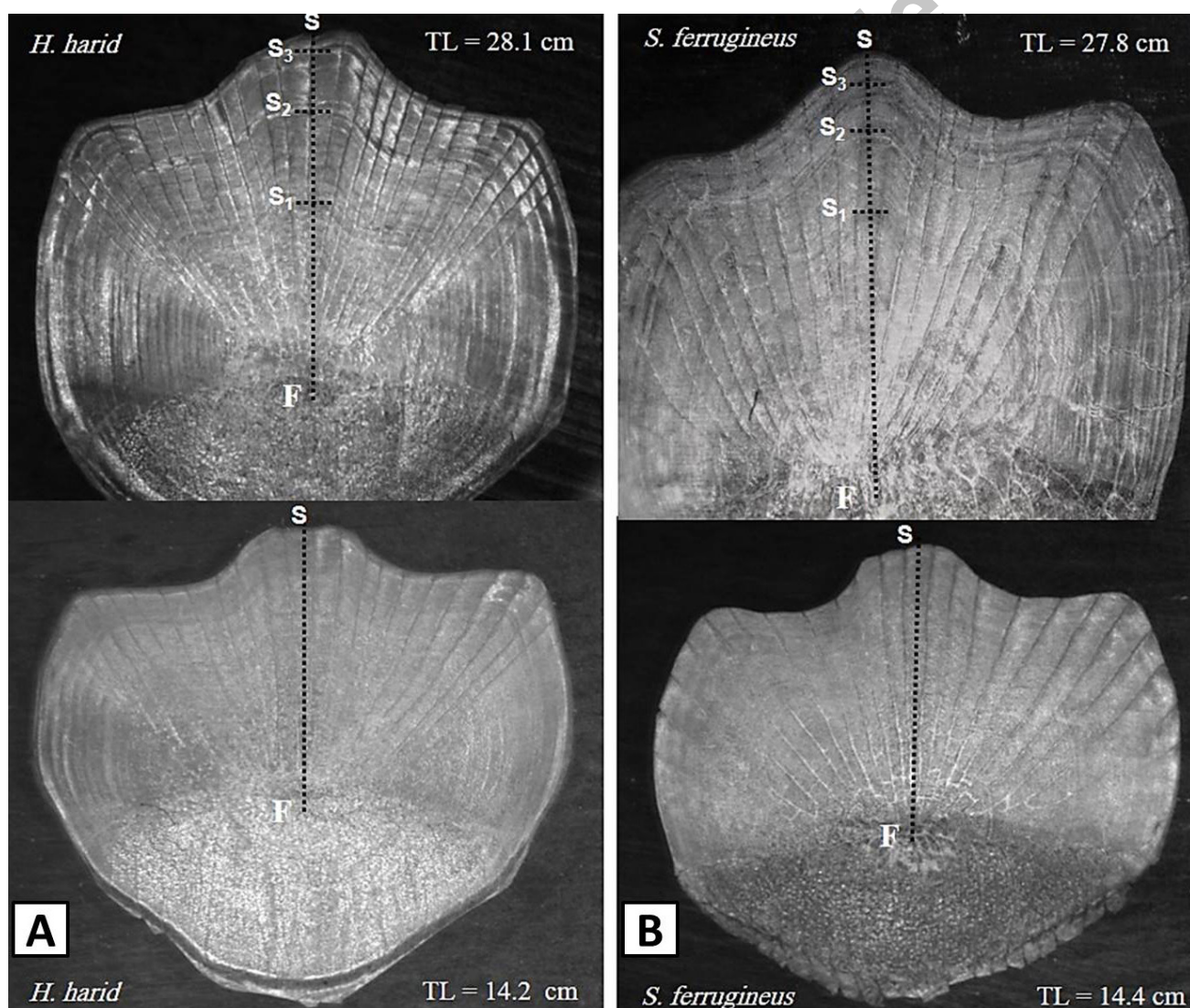


Fig. 11. The annual check marks (S₁, S₂, S₃) on the scales of *H. harid* (A) and *S. ferrugineus* (B) collected from Jeddah fisheries (F, focus; S, scale radius).

Table V.- Growth parameters of *H. harid* and *S. ferrugineus* in the Red Sea estimated by different Authors.

Reference	<i>H. harid</i>				<i>S. ferrugineus</i>			
	L_{∞}	K	t_0	ϕ	L_{∞}	K	t_0	ϕ
Present study (Red Sea–Saudi Arabia)	54.0436	0.168	-0.7073	2.69	51.238	0.170	-0.8892	2.65
Ali <i>et al</i> (2011) (Red Sea- Saudi Arabia)	44.59	0.17	-1.52	2.53	61.4	0.1	-2.20	2.60
Mehanna <i>et al</i> (2014) (Red Sea- Egypt)	57.16	0.23	-0.69	2.88*	-	-	-	-

* Estimated from the available L_{∞} and K values.

Table VI.- Length-weight relationship parameters of *H. harid* and *S. ferrugineus* in the Red Sea estimated by different Authors.

Reference	<i>H. harid</i>				<i>S. ferrugineus</i>			
	Length range	a	b	r^2	Length range	a	b	r^2
Present study (Red Sea–Saudi Arabia)	12.4 - 48.2 TL	0.027	2.82	0.985	13.2 - 48.5 TL	0.020	2.97	0.989
Ali <i>et al</i> (2011) (Red Sea- Saudi Arabia)	15.9 – 31.0 SL	0.023	2.99	-	12.5 – 31.6 SL	0.019	3.09	-
Mehanna <i>et al.</i> (2014) (Red Sea- Egypt)	17.0 – 50.0 TL	0.018	2.932	0.975	-	-	-	-

TL, total length; SL, standard length.

Growth in length

The growth rates estimated from the average back-calculated lengths at ages for sexes combined (pooled data) indicated that the maximum rate of growth in length was attained during the first year of life for both *H. harid* (13.82 cm) and *S. ferrugineus* (14.59 cm). During the second year, the annual increment was reduced to less than half of its value in the first year for *H. harid* (6.9 cm) and *S. ferrugineus* (6.5 cm), followed by gradual decrease during the next years. This trend of growth in length is more or less similar to those observed and reported in previous studies on the same two species in the Red Sea (Ali *et al.*, 2011; Mehanna *et al.*, 2014,) and other scarid species (Choat *et al.*, 1996; Taylor and Choat, 2014).

Growth parameters

Considerable variability was found among the von Bertalanffy growth parameters estimated by different authors based on back-calculated lengths-at-ages, where scales were used for age determination for *H. harid* and *S. ferrugineus* in the Red Sea (Table V). This variability might be because of different back-calculated lengths at ages calculated using different back-calculation methods. Collecting scales from different body sites, measuring scales at different angles, and poor representation of all size groups in the samples may lead to a wide variation in the values of the regression analyses parameters used in the back-calculation methods (Carlander, 1982; Hirschhorn and Small, 1987).

For *H. harid*, the growth parameters estimated in the present study are comparable to those estimated by Mehanna *et al* (2014). The larger values of the asymptotic length and growth coefficient may be due to the slightly

wider length range (17–50 cm) with fewer age groups assigned (8 age groups compared to 12 age groups in the present study).

For *S. ferrugineus*, Ali *et al.* (2011) estimated an extremely high asymptotic length (61.4 cm, standard length) with a corresponding very low growth coefficient (0.1 yr⁻¹) compared to the maximum observed length they recorded (31.6 cm). In the present study, the estimated asymptotic length (51.2 cm total length) was close to the maximum observed length (48.5 cm) and much smaller than that estimated by Ali *et al.* (2011).

However, both values of the growth coefficient for *H. harid* (0.168 year⁻¹) and *S. ferrugineus* (0.1704 year⁻¹) indicate that both species are moderate growth species (Branstetter, 1987). *H. harid* has slightly larger growth performance than that of *S. ferrugineus* due to the larger asymptotic length of the former (Table V).

Length-weight relationship

From the power equation describing the relationship between fish length and weight, the fish growth can be determined to be isometric or not. When the exponent 'b' equals '3' then the growth is isometric. Values of 'b' lower than '3' mean negative allometric growth, whereas b values higher than '3' refer to positive allometric growth (Froese, 2006). As indicated in Table VI, the value of the exponent 'b' for *H. harid* was significantly lower than '3', reflecting a negative allometric growth for this species in Jeddah fisheries.

Mehanna *et al.* (2014) predicted a negative allometric growth for the same species having comparable size range and length type (total length) in the Egyptian Red Sea. Ali *et al.* (2011) used smaller size range and length

type (standard length) for the same species in Jeddah fisheries estimated the 'b' value to be 2.99 which is not significantly different from the isometric growth ($b = 3$). Also, Ali *et al.* (2011) estimated higher 'b' value for *S. ferrugineus* (3.09) compared to that found in the present study (2.97). However, Carlander (1977) showed that using the standard-length measurements results in higher condition factors than that when using measurements of larger length types (fork and total length). This, in addition to the narrow size range, may be the reason behind the larger 'b' values obtained by Ali *et al.* (2011) compared to that obtained in the present study.

Exploitation and maximum yield per recruit

The obtained results of mortality coefficients listed in Table III indicate that the stocks of both species are subject to a fishing mortality that is almost double the amount of natural deaths. To assess the stock status of both species under the current level of fishing mortality, the Beverton and Holt's model (Beverton and Holt, 1957) was applied to estimate the yield per recruit at various levels of fishing mortality giving the yield per recruit curve for each species (Fig. 10).

For *H. harid*, it is evident from the results listed in Table IV and shown in Figure 10, that the current fishing mortality rate $F_{cur} = 0.67 \text{ year}^{-1}$ is higher than both values of $F_{max} = 0.401 \text{ year}^{-1}$ and $F_{0.1} = 0.245 \text{ year}^{-1}$, which means that the stock of this species is currently overexploited. Increasing the age at first capture from 1.93 to 2.99 year increased the yield and biomass per recruit at the current level of fishing mortality from 108.1 and 161.4 g (12.4% of the virgin (un-fished) biomass per recruit $B_{\sqrt{R}} = 1305.29 \text{ g}$) to 129.0 and 192.5 g (14.7% of $B_{\sqrt{R}}$), respectively.

For *S. ferrugineus*, the current level of fishing mortality $F_{cur} = 0.471 \text{ year}^{-1}$ is higher than both values of $F_{max} = 0.434 \text{ year}^{-1}$ and $F_{0.1} = 0.307 \text{ year}^{-1}$, reflecting a current overexploitation of the stock of this species in Jeddah fisheries. Similarly, when the age at first capture increased from 1.88 to 3.04 year, the yield and biomass per recruit at the current level of fishing mortality increased from 137.6 and 292.1 g (19.3% of $B_{\sqrt{R}} = 1516.2 \text{ g}$) to 153.6 and 326.0 g (21.5% of $B_{\sqrt{R}}$), respectively.

For both species, the levels of biomass per recruit at the current levels of fishing mortality may be not enough to provide sufficient recruitment to the fishery. Goodyear (1993) indicated that the recruitment process is dependent on the spawning stock biomass per recruit (SSBR). He also reported that the spawning potential ratio $SPR = \frac{SSBR_{fished}}{SSBR_{unfished}}$ which is proportional to $\frac{B/R_{fished}}{B/R_{unfished}}$ expressed in the Beverton and Holt's yield per recruit model, should be between 20–30% to obtain the maximum or near maximum yield per recruit. Thus, we

recommend reducing the current level of fishing mortality to that of the target reference point $F_{0.1} = 0.453 \text{ year}^{-1}$ after increasing the age at first capture from 1.93 year to 2.99 year to get a biomass per recruit of 279.7 g (21.4 %) for *H. harid*. For *S. ferrugineus*, we recommend reducing the fishing mortality from the current level to that of the target reference point $F_{0.1} = 0.466 \text{ year}^{-1}$ after increasing the age at first capture from 1.88 year to 3.04 year to get a biomass per recruit of 329.1 g (21.7 %).

However, increasing the age at first capture means improving the fishing gear selectivity to avoid the capture of young immature fish; by increasing the mesh size of the fishing net or/and avoiding the fishing ground having the young immature fish. Gabr and Mal (2016) recommended the use of trammel nets with 62 mm inner-panel mesh size to catch *H. harid* of a mean selection length of 24.46 cm total length, which is very close to that recommended in the present study to obtain the target yield and biomass per recruit.

CONCLUSION

Currently, the stocks of both species *Hipposcarus harid* and *Scarus ferrugineus* in Jeddah fisheries are overexploited. For both species, the levels of biomass per recruit at the current levels of fishing mortality may be not enough to provide sufficient recruitment to the fishery. Thus, we recommend reducing the current level of fishing mortality to that of the target reference point $F_{0.1} = 0.453 \text{ year}^{-1}$ after increasing the age at first capture from 1.93 year to 2.99 year to get a biomass per recruit of 279.7 g (21.4 % of the virgin stock biomass per recruit) for *H. harid*. For *S. ferrugineus*, we recommend reducing the fishing mortality from the current level to that of the target reference point $F_{0.1} = 0.466 \text{ year}^{-1}$ after increasing the age at first capture from 1.88 year to 3.04 year to get a biomass per recruit of 329.1 g (21.7 % of the virgin stock biomass per recruit).

ACKNOWLEDGMENTS

This project was funded by the Deanship of Scientific Research (DSR), at King Abdulaziz University, Jeddah, under Grant No. 461/150/1434. The authors, therefore, acknowledge with thanks DSR for technical and financial support.

Statement of conflict of interest

The authors declare no conflict of interest.

REFERENCES

Ali, T.E., Osman, A.M., Abdel-Aziz, S.H. and

- Bawazeer, F.A., 2011. Growth and longevity of the protogynous parrotfish, *Hipposcarus harid*, *Scarus ferrugineus* and *Chlorurus sordidus* (Teleostei, Scaridae), off the eastern coast of the Red Sea. *J. appl. Ichthyol.*, **27**: 840–846. <https://doi.org/10.1111/j.1439-0426.2010.01566.x>
- Alwany, M.A., Thaler, E. and Stachowitsch, M., 2009. Parrotfish bioerosion on Egyptian Red Sea reefs. *J. exp. Mar. Biol. Ecol.*, **371**: 170–176. <https://doi.org/10.1016/j.jembe.2009.01.019>
- Bellwood, D.R., 1994. A phylogenetic study of the parrotfishes family Scaridae (Pisces: Labroidae), with a revision of genera. *Rec. Aust. Mus. (Suppl.)*, **20**: 1–86. <https://doi.org/10.3853/j.0812-7387.20.1994.51>
- Beverton, R.J.H. and Holt, S.J., 1957. *On the dynamics of exploited fish populations*. Fishery Invest, Ministry of Agriculture of Fish and Food, G.B. London, pp. 533. <https://trove.nla.gov.au/work/13338365>
- Boutson, A., Mahasawasde, C., Mahasawasde, S., Tunkijanakij, S. and Arimoto, T., 2009. Use of escape vents to improve size and species selectivity of collapsible pot for blue swimming crab *Portunus pelagicus* in Thailand. *Fish. Sci.*, **75**: 25–33. <https://doi.org/10.1007/s12562-008-0010-z>
- Branstetter, S., 1987. Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. *Environ. Biol. Fish.*, **19**: 161–173. <https://doi.org/10.1007/BF00005346>
- Cadima, E.L., 2003. *Fish stock assessment manual*. FAO Fisheries Technical Paper 393, FAO, pp. 161. <http://www.fao.org/3/a-x8498e.pdf>
- Carlander, K.D., 1982. Standard intercepts for calculating lengths from scale measurements for some centrarchid and percoid fishes. *Trans. Am. Fish. Soc.*, **111**: 332–336. [https://doi.org/10.1577/1548-8659\(1982\)111<332:SIFCLF>2.0.CO;2](https://doi.org/10.1577/1548-8659(1982)111<332:SIFCLF>2.0.CO;2)
- Ceyhan, T., Samsun, O. and Akyol, O., 2019. Age, growth and mortality of Garfish, *Belone euxini* Günther, 1866 in the Central Black Sea, Turkey. *Pakistan J. Zool.*, **51**: 273–278. <http://dx.doi.org/10.17582/journal.pjz/2019.51.1.273.278>
- Choat, J.H. and Robertson, D.R., 1975. Protogynous hermaphroditism in fishes of the family Scaridae. In: *Intersexuality in the animal kingdom* (ed. R. Reinboth). Springer, Berlin, Heidelberg, pp. 263–283. https://doi.org/10.1007/978-3-642-66069-6_26
- Choat, J.H. and Bellwood, D.R., 1991. Reef fishes- their history and evolution. In: *The ecology of fishes on coral reefs* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 39–66. <https://doi.org/10.1016/B978-0-08-092551-6.50008-8>
- Choat, J.H., Axe, L.M. and Lou, D.C., 1996. Growth and longevity in fishes of the family Scaridae. *Mar. Ecol. Progr. Ser.*, **145**: 33–41. <https://doi.org/10.3354/meps145033>
- Clifton, K.E., 1995. Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. *Mar. Ecol. Progr. Ser.*, **116**: 39–46. <https://doi.org/10.3354/meps116039>
- Crone, P., Maunder, M., Valero, J., McDaniel, J. and Semmens, B., 2013. *Selectivity: Theory, estimation, and application in fishery stock assessment models*. Center for the Advancement of Population Assessment Methodology (CAPAM), Workshop Series Report 1, pp. 46. <https://doi.org/10.1016/j.fishres.2014.03.017>
- FAO, 2018. *Fishery and aquaculture statistics. Global Capture Production 1950-2016 (FishstatJ)*. FAO Fisheries and Aquaculture Department, Rome. www.fao.org/fishery/statistics/software/fishstatj/en
- Ford, E., 1933. An account of the herring investigations conducted at Plymouth during the years from 1924 to 1933. *J. Mar. Biol. Assoc. U.K.*, **19**: 305–384. <https://doi.org/10.1017/S0025315400055910>
- Fowler, A.J., 1995. Annulus formation on otoliths of coral reef fish-a review. In: *Recent developments in fish otolith research* (eds. D.H. Secor, J.M. Dean and S.E. Campana). University of South Carolina Press, Columbia, pp. 45–63.
- Francis, R.I.C.C., 1990. Back-calculation of fish length: a critical review. *J. Fish Biol.*, **36**: 883–902. <https://doi.org/10.1111/j.1095-8649.1990.tb05636.x>
- Froese, R., 2006. Cube law, condition factor, and weight-length relationships: History, meta-analysis and recommendations. *J. appl. Ichthyol.*, **22**: 241–253. <https://doi.org/10.1111/j.1439-0426.2006.00805.x>
- Gabr, M.H. and Mal, A.O., 2016. Trammel net size-selectivity for *Hipposcarus harid* (Forsskal, 1775) and *Lethrinus harak* (Forsskal, 1775) in coral reef fisheries of Jeddah, Saudi Arabia. *Egyptian J. aquat. Res.*, **42**: 491–498. <https://doi.org/10.1016/j.ejar.2016.09.005>
- Gabriel, W.L. and Mace, P.M., 1999. *A review of biological reference points in the context of the precautionary approach*. Proceedings of the 5th annual NMFS National Stock Assessment Workshop, NOAA Tech. Memo., NMFS-F/SPO-40. <https://www.st.nmfs.noaa.gov/Assets/stock/>

- [documents/workshops/nsaw_5/gabriel_.pdf](#)
- Gayanilo, Jr. F.C., Sparre, P. and Pauly, D., 2005. *User's guide: FAO-ICLARM stock assessment tools II (FiSAT II)*, revised version. FAO Computerized Information Series (Fisheries) No. 8, revised version. FAO, Rome, pp. 168.
- Goodyear, C.P., 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. In: *Risk evaluation and biological reference points for fisheries management* (eds. S.J. Smith, J.J. Hunt and D. Rivard). Canadian Special Publication of Fisheries and Aquatic Sciences, pp. 67-81.
- Goodyear, C.P., 1995. Mean size at age: An evaluation of sampling strategies using simulated red grouper data. *Trans. Am. Fish. Soc.*, **124**: 746–755. [https://doi.org/10.1577/1548-8659\(1995\)124<0746:MSAAAE>2.3.CO;2](https://doi.org/10.1577/1548-8659(1995)124<0746:MSAAAE>2.3.CO;2)
- Hamel, O.S., 2015. A method for calculating a meta-analytical prior for the natural mortality rate using multiple life history correlates. *ICES J. Mar. Sci.*, **72**: 62–69. <https://doi.org/10.1093/icesjms/fsu131>
- Hirschhorn, G. and Small, G.J., 1987. Variability in growth parameter estimates from scales of Pacific cod based on scale and area measurements. In: *Age and growth of fish* (eds. R.C. Summerfelt and G.E. Hall). Iowa State University Press, Ames, pp. 147-157.
- Hoggarth, D.D., Abeyasekera, S., Arthur, R.I., Beddington, J.R., Burn, R.W., Halls, A.S., Kirkwood, G.P., McAllister, M., Medley, P., Mees, C.C., Parkes, G.B., Pilling, G.M., Wakeford, R.C. and Welcomme, R.L., 2006. *Stock Assessment for fishery management – A Framework guide to the stock assessment tools of the fisheries management science programme (FMSP)*. FAO Fisheries Technical Paper 487, pp. 261. <http://www.fao.org/3/a-a0486e.pdf>
- Jensen, A.L., 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Can. J. Fish. aquat. Sci.*, **53**: 820–822. <https://doi.org/10.1139/f95-233>
- Lee, R.M., 1920. A review of the methods of age and growth determination in fishes by means of scales. *Fish. Investig. Lond. Ser.*, **24**: 1–32.
- Lokrantz, J., Nystrom, M., Thyresson, M. and Johansson, C., 2008. The non-linear relationship between body size and function in parrotfishes. *Coral Reefs*, **27**: 967-974. <https://doi.org/10.1007/s00338-008-0394-3>
- Lou, D.C., 1992. Validation of annual growth bands on the otolith of tropical parrotfishes (*Scarus schlegelii* Bleeker). *J. Fish. Biol.*, **41**: 775–790. <https://doi.org/10.1111/j.1095-8649.1992.tb02706.x>
- Mathews, C.P. and Samuel, M., 1990. Using the growth performance index ϕ' to choose species for aquaculture: an example from Kuwait. *Aquabyte*, **3**: 2-4.
- Mehanna, S.F., Abu-Elregal, M. and Abdel-Maksoud, Y.A., 2014. Age and growth based on the scale readings of the two scarid species *Hipposcarus harid* and *Chlorurus sordidus* from Hurgada fishing area, Red Sea, Egypt. *Int. J. mar. Sci.*, **4**: 1-6.
- Pauly, D., 1983. *Some simple methods for the assessment of tropical fish stocks*. FAO Fisheries Technical Paper 234, FAO, Rome, pp. 52.
- Pauly, D., 1984a. *Fish population dynamics in tropical water: A manual for use with programmable calculators*. ICLARM Studies and Reviews 8, International Center for Living Aquatic Resources Management, Manila, Philippines.
- Pauly, D., 1984b. Length-converted catch curves. A powerful tool for fisheries research in the Tropics (Part 1). *ICLARM Fishbyte*, **1**: 9-13.
- Pauly, D. and Munro, J.I., 1984. Once more on the comparison of growth in fish and invertebrates. *FishByte*, **2**: 21-23.
- Pierce, C.L., Rasmussen, J.B. and Leggett, W., 1996. Back-calculation of fish length from scales: Empirical comparison of proportional methods. *Trans. Am. Fish. Soc.*, **125**: 889-918. [https://doi.org/10.1577/1548-8659\(1996\)125<0889:BCOFLF>2.3.CO;2](https://doi.org/10.1577/1548-8659(1996)125<0889:BCOFLF>2.3.CO;2)
- Randall, J.E., 2007. *Reef and shore fishes of the Hawaiian Islands*. University of Hawai'i Sea Grant College Program, Honolulu. ISBN 978-1-929054-03-9 [https://doi.org/10.1643/0045-8511\(2007\)2007\[775:RASFOF\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2007)2007[775:RASFOF]2.0.CO;2)
- Russ, G.R., 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. 11. Patterns of zonation of mid-shelf and outershelf reefs. *Mar. Ecol. Progr. Ser.*, **20**: 35-44. <https://doi.org/10.3354/meps020035>
- Russ, G.R. and St. John, J., 1988. *Diets, growth rates and secondary production of herbivorous coral reef fishes*. Proceedings of the Sixth International Coral Reef Symposium, pp. 37-43.
- Songrak, A., Bodhisuwan, W. and Thapanand-Chaidee, T., 2013. Selectivity of traps for blue swimming crab in Trang province. *MAEJO Int. J. Sci. Technol.*, **7**: 36-42.
- Sparre, P. and Venema, S.C., 1998. *Introduction to tropical fish stock assessment*, Part 1. Manual. FAO Fisheries Technical Paper. No. 306.1, Rev.

- 2, pp. 407. <ftp://ftp.fao.org/docrep/fao/w5449e/w5449e00.pdf>
- Stewart, J. and Ferrell, D.J., 2001. Mesh selectivity in the NSW demersal trap fishery. *Fish. Res.*, **59**: 379-392. [https://doi.org/10.1016/S0165-7836\(02\)00024-3](https://doi.org/10.1016/S0165-7836(02)00024-3)
- Taylor, B.M. and Choat, J.H., 2014. Comparative demography of commercially important parrotfish species from Micronesia. *J. Fish Biol.*, **84**: 383-402. <https://doi.org/10.1111/jfb.12294>
- van Rooij, J.M., Bruggemann, J.H., Videler, J.J. and Breeman, A.M., 1995. Plastic growth of the herbivorous reef fish *Sparisoma viride*—field evidence for a trade-off between growth and reproduction. *Mar. Ecol. Progr. Ser.*, **122**: 93-105. <https://doi.org/10.3354/meps122093>
- von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws 2). *Human Biol.*, **10**: 181-213.
- Walford, L.A., 1946. A new graphic method of describing the growth of animals. *Biol. Bull. Mar. Biol. Lab.*, **90**: 141-147. <https://doi.org/10.2307/1538217>
- Warner, R.R. and Downs, I.F., 1977. *Comparative life histories: Growth vs reproduction in normal males and sex-changing hermaphrodites of the striped parrotfish, Scarus croicensis*. Proceeding of the 3rd International Coral Reef Symposium, pp. 275-281.
- Williams, T. and Bedford, B.C., 1974. The use of otoliths for age determination. In: *The ageing of fish* (ed. T.B. Baginal). Unwin Brothers Ltd., Surrey, pp. 114-123.
- Williams, D.B. and Hatcher, A.I., 1983. Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Mar. Ecol. Progr. Ser.*, **10**: 239-250. <https://doi.org/10.3354/meps010239>
- Westneat, M.W. and Alfaro, M.E., 2005. Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Mol. Phylogen. Evolut.*, **36**: 370-390. <https://doi.org/10.1016/j.ympev.2005.02.001>