Original Article

Age, growth and mortality of the thumbprint emperor (*Lethrinus harak*) in Zanzibar

Tumu A. Mussa [1,2,*], Saleh A.S.Yahya [1,4], Jose J. Castro [3], Leonard J. Chauka [1]

[1] Institute of Marine Sciences (IMS), University of Dar es Salaam, PO Box 668, Zanzibar, Tanzania

[2] Abdulrahman Al-Sumait University, PO Box 1933 Zanzibar, Tanzania

[3] University of Las palmas de Gran Canaria. Campus De Tafira. 36017. Las Palmas de Gran Canaria, Spain

[4] Deep Sea Fishing Authority (DSFA), P.O. Box 56, Fumba, Zanzibar, Tanzania.

Western Indian Ocean JOURNAL OF Marine Science

Open access

Citation:
Mussa TA, Yahya SAS, Castro JJ, Chauka LJ (2024) Age, growth and mortality of the thumbprint emperor (Lethrinus harak) in Zanzibar. Western Indian Ocean Journal of Marine Science 23(1): 9-18 [doi: 10.4314/wiojms.v23i1.2]

Received:
August 11, 2023

Accepted:
December 17, 2023

Published:
March 12, 2024

*** Corresponding author:**
mussa_tumu@yahoo.com

Abstract
The growth parameters of *Lethrinus harak* from Zanzibar were studied from 308 samples collected between June 2019 and May 2020 at Unguja Ukuu and Mkokotoni landing sites. Growth rings counted on whole otoliths formed annually, with opaque margins generated in December to February and hyaline rings in March to November. Ring counts revealed that most fish were between three and four years old, with mean lengths of 17.7 and 21.4 cm, respectively. Some specimens were five to seven years old, measuring 24.2 to 28.2 cm, on average. The growth parameters were estimated as L_∞ = 34.22 cm, K = 0.25 year^{-1}, and t_0 = 0.00. The total mortality (Z) was estimated as 0.68 year^{-1}, natural mortality (M) was 0.65 year^{-1} using Pauly's equation, and fishing mortality (F) was 0.03 year^{-1}. The low estimate of exploitation rate (E) of 0.04 year^{-1} was almost certainly an underestimate, resulting from the absence of older (>8 years) large individuals, and younger (<3 years) small individuals in samples.

Keywords: *Lethrinus harak*, growth parameters, mortality rate

Introduction
Coastal communities in developing nations rely heavily on coral reef fisheries for their livelihood and food security (Johnson *et al.*, 2013). Coral reef habitats are, however, threatened by human activities and climate change (Cinner *et al.*, 2012; Lachs and Oñate-Casado, 2020). In East Africa, human-induced pressure on coral reefs has been well documented (Wilkinson, 2008; Hoegh-Guldberg, 2011) and the associated loss of ecosystem services linked to the coral reefs is of concern (Cinner *et al.*, 2011). Inadequate monitoring and sparse scientific data on key exploited species hinder management and conservation efforts in the region.

Local communities in Zanzibar are heavily dependent on small-scale fisheries for their livelihoods (Jiddawi and Khatib, 2007; Jeppesen and Richmond, 2016). Small-scale fisheries of Unguja Island are representative of the multi-species artisanal fisheries common along the eastern African coastline, with few commercial fleets present near the coast. Fisheries are characterized by monsoon cycles, and inshore fisheries using multiple gear types land mostly reef-associated species (e.g., Siganids, Lethrinids, Octopus), small pelagic fishes (e.g., Engraulids) and larger pelagic species (Scomberids) (Jiddawi and Öhman, 2002). Depletion of fishery resources in Tanzania has been attributed to overfishing and use of destructive fishing methods such as beach seine, stick and spear fishing and poison, locally known as *juya*, *mkuki/kijiti* and *utupa* respectively (Jiddawi and Öhman, 2002; Khatib and Jiddawi, 2010).

Landings of emperors have increased annually in parts of the Western Indian Ocean, because of high demand (Kulmiye *et al.*, 2002; Vasanthrajan *et al.*, 2012). The commercial importance of Lethrinids have resulted in several studies of their life history (Grandcourt, 2002; Kulmiye *et al.*, 2002; Pilling *et al.*, 2003; Ebisawa, 2006; Ebisawa and Ozawa, 2009; Currey *et al.*, 2013; Trianni, 2016). Despite global efforts to assess the stocks of Lethrinid species, such information is lacking in Tanzania.

The thumbprint emperor (*Lethrinus harak*) is a widely distributed tropical reef species (Midway *et al.*, 2018) and an important food source in Tanzania (Kimirei *et al.*, 2013; Midway *et al.*, 2018). Improved management is however required to facilitate sustainable fishing practices. Age, growth rate, and mortality rate are three of the most influential life history characteristics controlling the productivity of fish populations (Mendoza, 2006). This information is important in assessments of stock status, on which management strategies typically rely (Ebiswa and Ozawa, 2009). The aims of this study were to use catch-at-length data and analysis of otolith ring counts to estimate the age distribution of *L. harak*, growth and mortality rates (Pilling *et al.*, 2003; Vieira, 2023).

Methodology

Study site and sampling

This study was conducted in Zanzibar (Zanzibar archipelago, Tanzania) (Fig. 1). Fish samples were obtained at landing sites on the southern (Unguja Ukuu landing site) and northern coasts (Mkokotoni landing site) of Unguja Island. A total of 308 *L. harak* specimens were randomly purchased from fishers over a 12-month period from June 2019 to May 2020. Fish samples were immediately frozen after purchase and transferred to a laboratory for analysis.

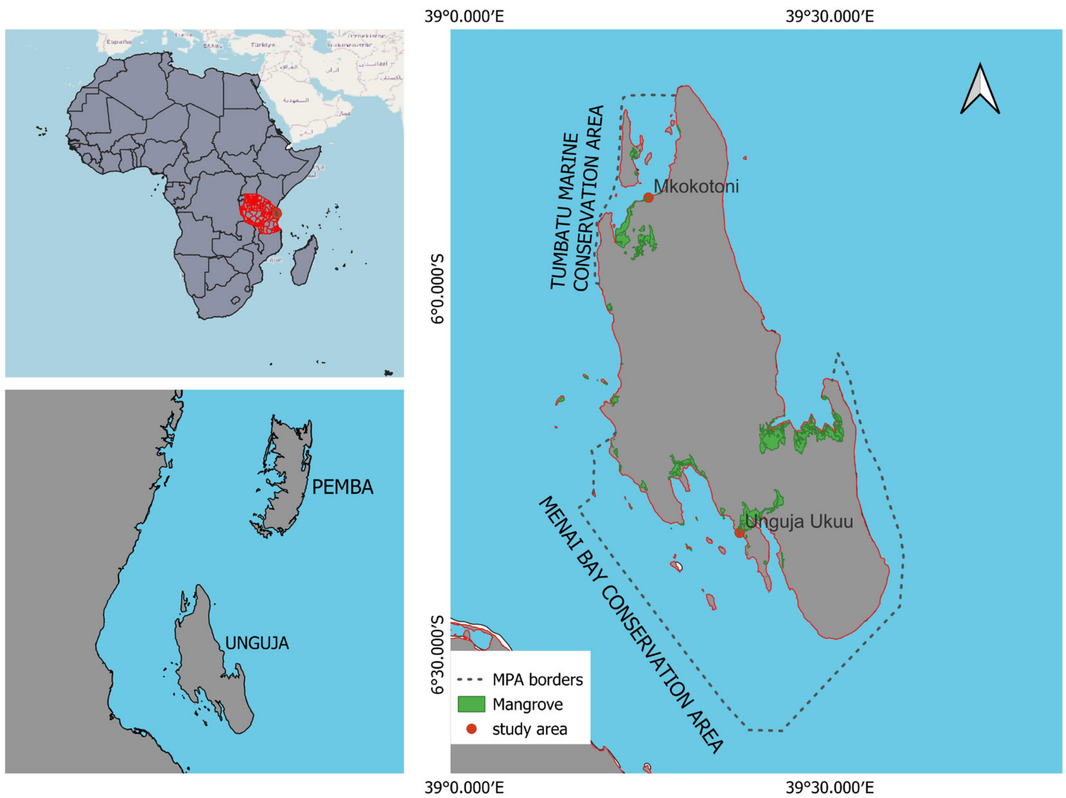

Figure 1. Map of Unguja Island (Zanzibar archipelago, Tanzania) showing the main sampling sites.

Measurements of length and weights

The total length (TL ± 1 cm) and total body weight (TW ± 1 g) of each fish was measured using a measuring board and balance. Otoliths were extracted via a horizontal cranial incision, cleaned, and stored in 70 % ethanol (Matta and Kimura, 2012). In the laboratory, otoliths were dried through air-exposure, and length (± 0.1 mm) and weight (± 0.001 g) measurements determined with a vernier caliper and electronic balance. The yearly age rings (annuli) were visualized using a light microscope equipped with a C-P8 opticam PRO8 digital camera. The age readings were carried out by one person after calibration. For fish larger than 25 cm TL, the otoliths were polished using P500 and P800 polish papers to identify the growth annuli clearly. To determine if hyaline and opaque rings were formed each year, the edges of otolith samples collected monthly were examined, with hyaline margins appearing as dark and opaque margin as white under reflected light.

Data analysis

Age determination

Age was determined from otolith measurements and length frequency analysis. Growth rings were counted using a reflected light stereoscopic microscope. To analyse the cohorts using length frequency data, a modal progression analysis (MPA) was performed by the separation of normal distributed components (NORMSEP) method using FiSAT-II software (Gayanilo *et al*., 2005). Length data of *L. harak* were available by month and grouped into 2-cm intervals.

Length weight relationship and sex ratio

The R-core team (2020), software version (4.0.3) was used to determine the potential relationships between fish TW and TL using the power function:

$$W = a*TL^{b}$$

Where *W* is wet weight (g), *TL* is total length (cm), *a* is the multiplicative factor and *b* is the exponent ($b > 1$). When $b = 3$, the growth pattern is isometric, positive allometric when $b > 3$, and negative allometric when $b < 3$ (Heydarnejad, 2009, Phillips *et al.,* 2018). The parameters *a* and *b* were estimated using the non-linear least square estimation procedure. The relationship between otolith weight and fish age was described using a linear relationship (Heydarnejad, 2009)

Growth rate

A growth model provides information about fish age in relation to their length and weight and is often viewed as the end product of growth analysis (Jones, 2000). The Von Bertalanffy Growth Formula (VBGF) was used:

$$Lt = L_{\infty} [1-e^{-k (t-t0)}]$$

Where Lt = mean length at age t, L_{∞} = asymptotic length, K = growth coefficient, determining the rate of change in the length increment, t = age of the species, and t_0 = the hypothetical age at which the length is zero. The growth parameters (L_{∞}, K and t_0) were estimated for males and females separately, and for both sexes combined, using length-at-age data obtained from otolith measurements. The growth performance index, Phi-prime (Ø), was calculated from Munro and Pauly (2012) as follows:

$$Ø = \log K + 2\log L_{\infty}$$

Where L_{∞} and K are asymptotic length and rate constants from VBGF respectively.

Mortality rate

The total mortality (*Z*) estimate includes natural mortality and fishing mortality which is calculated as the sum of fishing mortality (*F*) and natural mortality (*M*) (Jayasankar, 2014), given as:

$$Z = M + F$$

Where *Z* is total mortality, *M* is natural mortality and *F* is fishing mortality. Total mortality (*Z*) was calculated using a length converted catch curve using the FiSAT II software with age-based data. The model explains the relationship between the total mortality coefficient and the mean length of the exploited portion of the fish stock which was calculated as:

$$Z = K (L_{\infty} - Lmean) / (L_{\infty} - L')$$

L mean is the mean length of a sample representing a steady state in a population, and *L'* is a cut-off length or the lower limit of smallest length class included.

Natural mortality (M)

Natural mortality was obtained using Paulys' equation (Pauly, 1980) expressed as:

$$\log M = 0.654 \log K - 0.28 \log L_{\infty} + 0.463 \log T$$

Where *T* is the environmental temperature.

Fishing mortality (F)

Fishing mortality provides a value for the level of depletion in a fish stock that results from fishing activities, obtained from:

$$F = Z - M$$

Exploitation rate (E)

The exploitation rate was calculated as the ratio between the fishing mortality coefficient (*F*) and total mortality coefficient (*Z*), which is equal to the fraction of the stock taken by fishing activities over time.

$$E) = F/Z$$

For optimally exploited stocks, $E = 0.5\ year^{-1}$

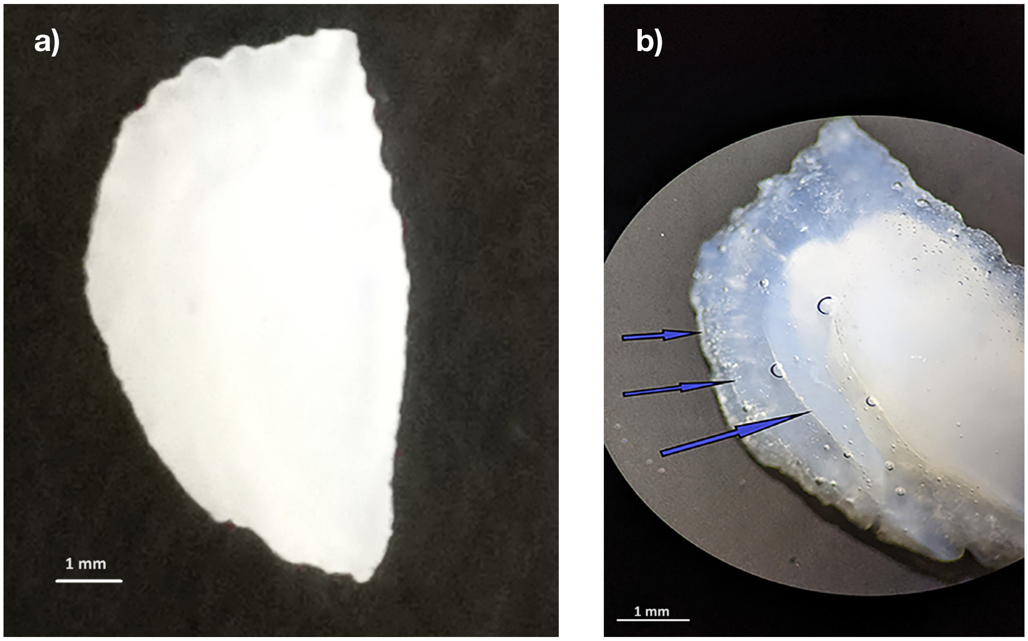

Figure 2. Otolith image concave side up. (a) without microscope and (b) with microscope under reflected light with dark background (2.0 magnification); arrows indicate annulus rings.

Results

Of 308 individuals investigated, 180 (58.4 %) were males and 128 (41.6 %) were females, with the smallest and largest lengths being 14.3 and 29.6 cm TL respectively. The smallest otolith was 0.051 mm long and weighed 0.028 g, and the largest otolith measured 0.88 mm and weighed 0.048 g. The otoliths were generally white in colour and elongated in shape, concave toward the anterior apex and semi rounded in shape toward the posterior apex (Fig. 2a). The whole otoliths showed clear rings when visualized with a reflected light stereoscopic microscope with a dark background (Fig. 2b).

Age estimates from otolith readings

From the yearly otolith annuli readings of the 308 fishes, 129 (41.9 % - comprising 100 males and 29 females) were three years old, 104 (33.8 % - 66 males and 38 females) were four years old, 33 (10.7 % - 7 males and 26 females) were five years old, 29 (9.4 % - 5 males and 24 females) were six years old and 13 individuals (4.2 % - 2 males and 11 females) were seven years old. Individuals younger than three and older than seven years were absent. The mean lengths at ages three to seven years were 17.7 cm, 21.0 cm, 24.2 cm, 25.9 cm and 28.2 cm, respectively. The marginal observation of otoliths showed that the opaque and hyaline rings were formed throughout the year with monthly variations. Individuals with opaque margins were dominant in December, January and February and hyaline margins during the remainder of the months (March to November).

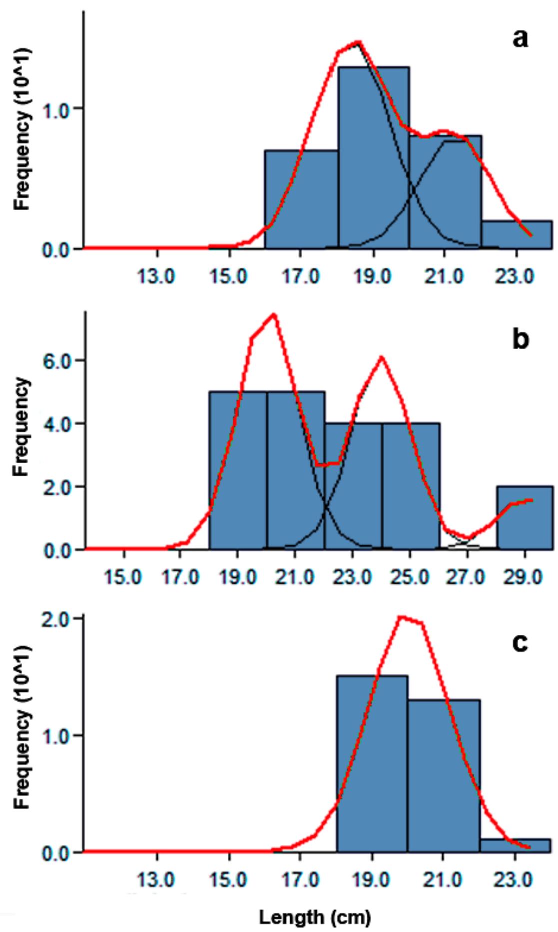

Figure 3. NORMSEP model showing population cohorts of *Lethrinus harak*. (a) two cohorts in January; (b) three cohorts in November; (c) one cohort in December.

Age group from length frequency data

The results of the NORMSEP model assessed using FiSAT II showed two cohorts in June to October 2019, and in January, February and May 2020. In November 2019 and March 2020 three cohorts were detected, and one in December and April, respectively (Fig. 3).

Length-weight relationship

The length-weight relationship indicated that *L. harak* exhibits an isometric growth pattern (Fig. 4a, b and c) for both sexes, and for males and for females respectively, where both length and weight of fish increased at the same rate. Otolith weight was strongly correlated to age (p < 0.0001, R^2 = 0.5503, r =0.7418) (Fig. 4d). Otolith radius showed strong positive correlation to fish length (p < 0.000 1, R^2 = 0.6571, r = 0.81095) (Fig.4e). Key length/size at age for both sexes were also established corresponding to one year (June 2019-May 2020) (Table 1).

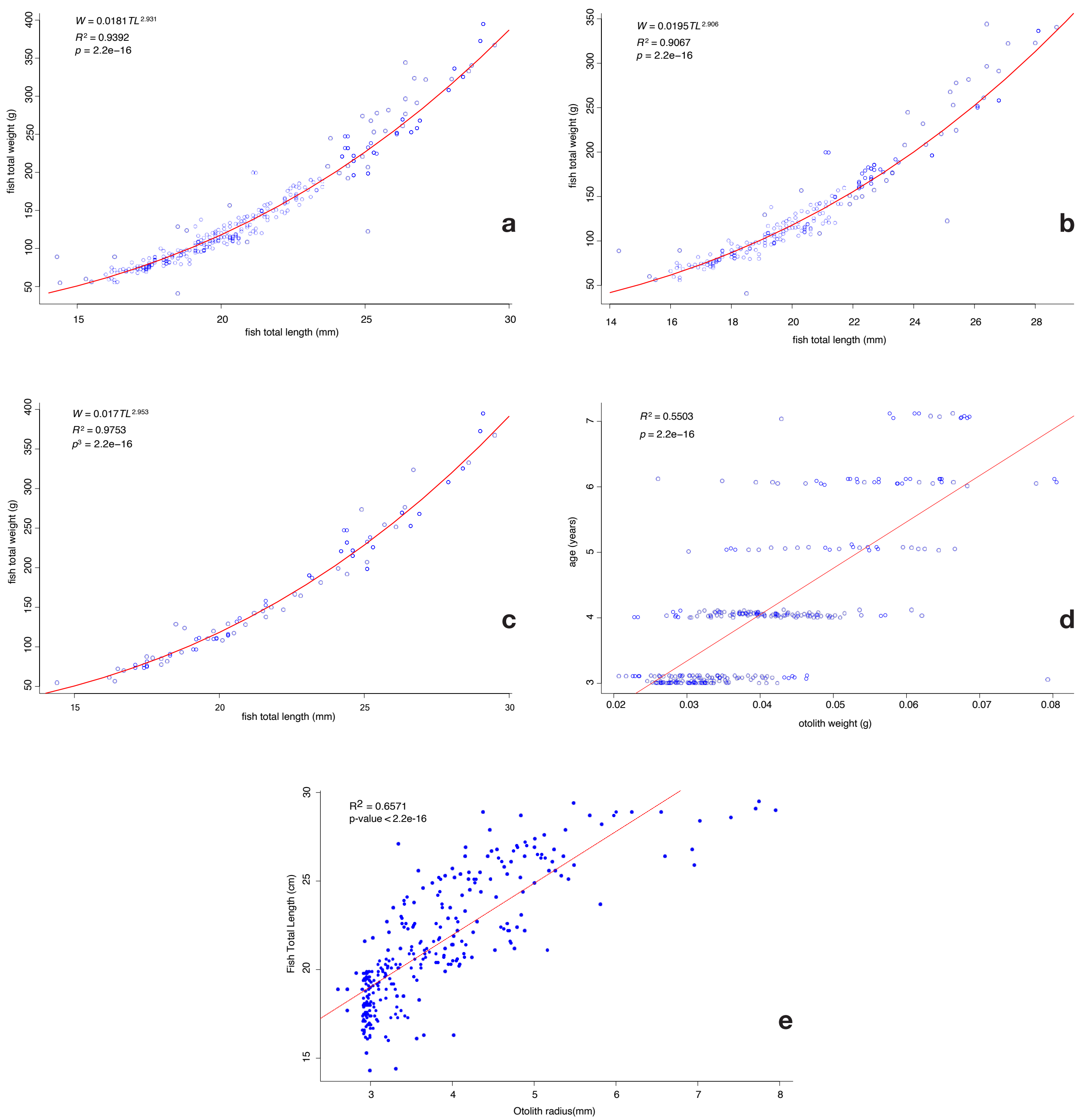

Figure 4. Isomeric growth curves for (a) both sexes, (b) males, and (c) females of *Lethrinus harak*. Linear regressions between (d) otolith weight and fish age and (e) otolith radius and fish length.

Table 1. Key length/size (cm) according to the age class for both sexes together of *Lethrinus harak,* corresponding to one year (June 2019-May 2020).

Total length	Age Classes							
TL in cm	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	
14			2					
15			2					
16			17					
17			31					
18			38					
19			39					
20				48	1			
21				23	2			
22				20	1			
23				7	3			
24				6	9			
25					13	11		
26					4	14	2	
27						2		
28						1	5	
29						1	6	
Mean Length (cm)			17.69	21.04	24.18	25.86	28.15	
Sd (cm)			1.17	1.21	1.47	0.95	1.07	
Total (N)			129	104	33	29	13	308
Percentage			41.88	33.77	10.71	9.42	4.22	100.00

Growth rate

Growth parameters calculated from length-at-age data (Table 2) found the asymptotic length $L\infty$ from data at both sampling sites to be larger than the maximum observed length (29.6 cm). Females had a higher asymptotic length (34.2 cm) than males (30.6 cm) which corresponded to a lower K value for females (K = 0.25) than males (K = 0.30) (Fig. 5a-c).

Mortality rates

The instantaneous total mortality rate (Z) calculated from the length converted catch curve (LCC) was 0.68 year^{-1} (95% C.I. of 0.38 - 0.99 and r^2 = 0.99) (Table 3), M was 0.65 year^{-1} and F was 0.03 year^{-1}. The exploitation rate was 0.04 year^{-1} (Table 3).

Discussion

The results obtained from this study indicate that the *Lethrinus harak* captured in Zanzibar waters are between three to seven years of age, although the fishery is dominated by fish of three and four years of age (75.7 %). The data on fish length do not deviate from Carpenter and Niem (2001) which showed *L. harak* individuals to be frequently fished at lengths between 20 to 30 cm (equivalent to 3 and 4 years of age). *L. harak* in the present study were all below seven years of age and the largest individual measured 29.6cm TL. *L. harak* can grow to a maximum of approximately 50 to 54 cm TL (Carpenter and Allen, 1989; Matthews *et al*., 2019), equivalent to an age of 12 to 15 years (Lasi, 2003; Trianni, 2016). The current analyses were therefore based on only a part of the population.

Like many coral reef fish species, *L. harak* was expected to have opaque and translucent zones formed during warmer and cool seasons respectively (Fowler, 2009). Such changes are associated with physiological change, growth rate differences and reproductive cycles (Fowler, 2009). For example, six Scaridae species develop opaque rings indicating high growth rates in summer (Choat *et al*., 1996). However, the current data showed the presence of both zones (opaque and hyaline) throughout the year; however, they dominated in different months. The opaque zones were observed in December, January and February, following the summer season and the hyaline zones during the rest of the months with full occurrence between July and September. This suggests that *L. harak* grows quicker in December to February, possibly associated with a change in water temperature and increase in primary production, caused by upwelling from north westerly winds. Coastal upwelling brings cold, nutrient-rich waters to the ocean surface from depth, increasing primary productivity (Hammond *et al*., 2022; Horii

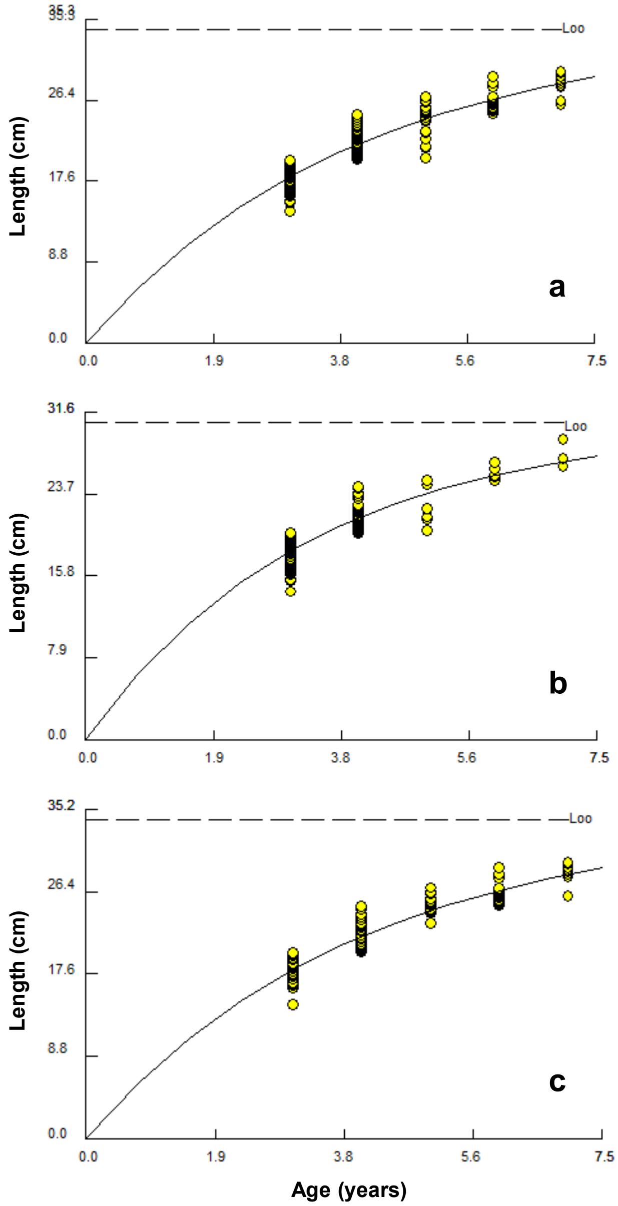

Figure 5. Von Bertalanffy Growth Function (VBGF) graphs for (a) both sexes, (b) males, and (c) females of *Lethrinus harak*.

et al., 2022). This tropical summer growth is contrary to other parts of the world where the opaque band in *Lethrinus* (incl. *L. harak*) occurred in August to December (Hilomen, 1997). Likewise, *Pargus auratus*, had less growth of opaque bands during winter (Ferrell *et al.*, 1992), compared to *L. nebulosus* in northern Great Britain where they had greater opaque zones that formed during the winter period (McPherson *et al.*, 1988). It should not be assumed that the opaque and translucent nature of bands in different species will be similar; though the pattern of wide and narrow banding tends to be consistent. The opacity and translucency of these bands varies considerably with species, light source and methodology. The ring deposition might also be affected by environmental or physiological stress such as spawning, migration, environmental fluctuations, hydro-meteorological conditions and age of fish (Hüssy and Mosegaard, 2004; Putnis and Korņilovs, 2008; Fablet *et al.*, 2011).

The values of *K* and L_∞ observed in this study suggested slow growth rates of *L. harak* in Zanzibar. This suggests that the *L. harak* do not get the opportunity to reach the asymptotic length, resulting in the removal of smaller individuals from the ecosystem, which can lead to detrimental effects. Decline in spawning biomass can cause negative effects to the point where recruitment is significantly impaired (Vasilakopoulos, 2011; Abdulrahman *et al,* 2021). Furthermore, domination of relatively young fish in catches, between three and four years of age, results in a population length structure that is heavily shifted toward younger age classes because of positive selection toward larger fish in the recent past; such size-selective fishing may have evolutionary consequences and may be difficult to reverse (Hsieh *et al.*, 2009). The observed values of *K* and L_∞ are closer to those presented by Ebisawa and Ozawa (2009), Trianni (2016) and Midway *et al.* (2018). The differences in both values between the current study and other studies may be attributed to geographical location, variation in recruitment pattern, seasonal changes in growth and size dependent selection (Hufnagl *et al.*, 2013). *L. harak* of age 12 years are commonly fished elsewhere (Lasi, 2003; Ebisawa and Ozawa, 2009), and therefore 3-year old fishes are still relatively young. Over-exploitation can result in scarcity of larger individuals, a likely scenario for *L. harak* in Zanzibar (Ali *et al.*, 2003; Beverton and Holt, 2012).

Table 2. The growth parameters of *Lethrinus harak* based on the Von Bertalanffy Growth Function (VBGF). Asymptotic length (L_∞) in cm, growth rate (*K*) in year^{-1}, and Phi prime Ø is an index of growth performance.

Species	Method	Sex	L∞	K	t0	Ø
L. harak	VBGF Plots	Both	34.25	0.25	0.00	2.46
	VBGF Plots	Males	30.57	0.30	0.00	2.44
	VBGF Plots	Females	34.22	0.25	0.00	2.46

Table 3. Mortality parameters, including the Exploitation rate (*E*), of *Lethrinus harak* in Zanzibar waters and from other studies. LCC = Length converted catch curve.

Model	Total mortality (Z) year^{-1}	Natural mortality (M) year^{-1}	Fishing mortality (F) year^{-1}	Exploitation rate (E)	Source	Place
LCC Age based	0.68	0.65	0.03	0.04	Present study	Tanzania/ Zanzibar
LCC	1.52	0.75	0.77	0.51	Lasi 2003	Fiji. Suva lagoon
Age based CC	0.239	0.381	-	-	Hilomen 1997	Lizard Island GBR
LCC	0.326-0.867	0.00-0.90	0.02-0.08	0.082-0.341	Trianni 2016	Saipan lagoon

The value of total mortality observed is less than that reported by Lasi (2003), higher than Hilomen (1997) and closer to Trianni (2016). Since the estimates of total mortality rate (*Z*) in this study show high contribution of natural mortality (*M*) and low contribution of fishing mortality (*F)*, total absence of older individuals could lead to biased estimates. The higher value of *M* could be attributed to sampling individuals of a smaller size, as they are known to have higher natural mortality from predation (Pauly, 1980). Hence the absence of older, larger individuals resulted in underestimation of Z and E. Theoretically, optimally exploited stocks have similar M and Z values, and close to 0.5 of its biomass (Pikitch *et al*., 2014). Even compared to smaller species with high recruitment variability and lower exploitation rates (E = 0.2; Pauly, 1984), the E of 0.04 year^{-1} estimated in this study is unrealistically low.

Overall, the relatively small asymptotic length in relation to the maximum length reported for *L. harak*, combined with the absence of individuals older than seven years of age from the sample (the lifespan of the species is estimated to be 15 years) may have led to over-estimation of M and an under-estimation of F. Thus, although the analysis suggested optimum exploitation (low F and low E), the absence of older, larger specimens in samples may actually reflect very high exploitation rates of *L. harak* in Zanzibar waters, something the model failed to show.

Conclusions

Lethrinus harak in Zanzibar waters is harvested at the age of three to four years, and no specimens aged between 8 and 15 years were available in the sample. Consequently, mortality estimates are biased, and the model output of low exploitation rate is in conflict with the general perception that *L. harak* is overexploited in Zanzibar. Future studies sampling deeper offshore reefs are required to investigate whether older individuals occur deeper, or whether they are completely absent from Zanzibar. Following that, a re-analysis of data, representing all size categories is recommended, to provide information for management of the species.

Acknowledgements

We would like to express our sincere gratitude to the staff of the Institute of Marine Sciences, University of Dar es Salaam, and fishers from Unguja Ukuu and Mkokotoni, Zanzibar for their cooperation and assistance. The study was financed by the Ministry of Blue Economy and Fisheries, Zanzibar, through their SWIOFish project.

References

Ali M, Nicieza A, Wootton RJ (2003) Compensatory growth in fishes: a response to growth depression. Fish and Fisheries 4 (2): 147-190

Beverton RJ, Holt SJ (2012) On the dynamics of exploited fish populations (Vol. 11). Springer Science and Business Media. 538 pp

Carpenter KE, Allen GR (1989) FAO species catalogue. Vol.9. Emperor fishes and large-eye breams of the world (family Lethrinidae). An annotated and illustrated catalogue of lethrinid species known to date. FAO Fisheries Synopsis. No. 125, Volume 9. FAO, Rome. 118 pp

Carpenter KE, Niem VH (2001) FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific, Volume 5: Bony Fishes Part 3 (Menidae to Pomacentridae). FAO, Rome. pp 2791-3380

Choat JH, Axe LM, Lou DC (1996) Growth and longevity in fishes of the family Scaridae. Marine Ecology Progress Series 145: 33-41

Cinner JE, Folke C, Daw T, Hicks CC (2011) Responding to change: Using scenarios to understand how socioeconomic factors may influence amplifying or dampening exploitation feedbacks among Tanzanian fishers. Global Environmental Change 21: 7-12

Cinner JE, McClanahan TR, Graham NAJ, Daw TM, Maina J, Stead SM, Wamukota A, Brown K, Bodin Ö (2012) Vulnerability of coastal communities to key impacts of climate change on coral reef fisheries. Global Environmental Change 22: 12-20

Currey LM, Williams AJ, Mapstone BD, Davies CR, Carlos G, Welch DJ, Simpfendorfer CA, Ballagh AC, Penny AL, Grandcourt EM, Mapleston A, Wiebkin AS, Bean K (2013) Comparative biology of tropical *Lethrinus* species (Lethrinidae): challenges for multi-species management. Journal of Fish Biology 82: 764-788

Ebisawa A (2006) Reproductive and sexual characteristics in five *Lethrinus* species in waters off Ryukyu Island. Journal of Ichthyological Research 53: 269-280

Ebisawa A, Ozawa T (2009) Life history trait if eight *Lethrinus* species from the local population in waters off Ryukyu Island. Journal of Fish Science 75: 553-556

Fablet R Pecquerie L, de Pontual H, Høie H, Millner R, Mosegaard H, Ooijman S (2011) Shedding light on fish otolith biomineralization using a bioenergetic approach. PLoS One 6 (11): 27055 [https:// doi.org/10.1371/journal.pone.0027055]

Ferrell DJ, Henry G W, Bell JD, Quartararo N (1992) Validation of annual mark in the otolith of young Snapper (*Pargus auratus*), Sparidae. Australian Journal of Marine and Freshwater Research 43: 1051-1055

Fowler A (2009) Age in years from otoliths of adult tropical fish. In: Green BS, Mapstone BD, Carlos G, Begg GA (eds) Tropical fish otoliths: Information for assessment, management and ecology. Reviews: Methods and Technologies in Fish Biology and Fisheries 11. Springer, Dordrecht [https://doi.org/10.1007/978-1-4020-5775-5_3]

Gayanilo FC, Sparre Jr, Pauly D (2005) FiSAT II–FAO-IRCLAM Stock assessment tool II, User's guide. FAO Computerized information series Fisheries (8). FAO, Rome.180 pp

Grandcourt EM (2002) Demographic characteristics of a selection of exploited reef fish from the Seychelles: preliminary study. Marine and Freshwater Research 53: 123-130

Hammond ML, Jebri F, Srokosz M Popova E (2022) Automated detection of coastal upwelling in the Western Indian Ocean: Towards an operational "Upwelling Watch" system. Frontiers in Marine Science 9: 950733

Heydarnejad MS (2009) Length-weight relationships for six freshwater fish species in Iran. Chinese Journal of Oceanology and Limnology 27 (1): 61-62

Hilomen VV (1997) Inter and intra-habitat movement patterns and population dynamics of small reef fishes of commercial and recreational significance. PhD thesis, James Cook University of Northern Queensland. 301 pp

Hoegh-Guldberg O (2011) Coral reef ecosystems and anthropogenic climate change. Regional Environmental Change 11: 215-227

Horii T, Siswanto E, Iskandar I, Ueki IK, Ando K (2022) Can coastal upwelling trigger a climate mode? A study on intra-seasonal-scale coastal upwelling off Java and the Indian ocean Dipole. Geophysical Research Letters 49 (15): 2022GL098733

Hsieh CH, Yamauchi A, Nakazawa T, Wang W F (2009) Fishing effects on age and spatial structures undermine population stability of fishes. Aquatic Sciences 72 (2): 165-178

Hufnagl M, Huebert KB, Temming A (2013) How does seasonal variability in growth, recruitment, and mortality affect the performance of length-based mortality and asymptotic length estimates in aquatic resources? ICES Journal of Marine Science 70 (2): 329-341

Hüssy K, Mosegaard H (2004) Atlantic cod (*Gadus morhua*) growth and otolith accretion characteristics modelled in a bioenergetic context. Canadian Journal of Fish and Aquatic Science 61: 1021-1031

Jayasankar J (2014) Estimation of mortality. Training manual on fish stock assessment and management. CMFRI, FRAD. 150 pp

Jeppesen G, Richmond M (2016) Investment prioritization for climate-resilient livelihoods and ecosystems in the coastal zones of Tanzania. Overview. World Bank, Washington, DC, USA [https://www.ndf.fi/sites/ndf.fi/files/attach/overview_publication_january_2016.pdf]

Jiddawi NS, Öhman MC (2002) Marine fisheries in Tanzania. Ambio: A Journal of Human Environmental Studies 31: 518-527

Jiddawi NS, Khatib H (2007) The fishery census of Zanzibar 2007. Department of Fisheries and Marine Resources. Report Series 4. Zanzibar Town. 61 pp

Johnson AE, Cinner JE, Hardt MJ, Jacquet J, McClanahan TR, Sanchirico JN (2013) Trends, current understanding and future research priorities for artisanal coral reef fisheries research. Fish and Fisheries 14: 281-292

Jones CM (2000) Fitting growth curve to retrospective size at -age -data. Fisheries Research 46: 123-129

Kimirei IA, Nagelkerken I, Trommelen M, Blankers P, Van Hoytema N, Hoeijmakers D, Huijbers CM, Mgaya YD, Rypel AL (2013) What drives ontogenetic niche shifts of fishes in coral reef ecosystems? Ecosystem 16: 783-796

Khatib H, Jiddawi NS (2010) Zanzibar fisheries frame survey report, 2010. Department of Fisheries and Marine Resources, Zanzibar. 80 pp

Kulmiye AJ, Ntiba MJ Kisia S (2002) Some aspects of the reproductive biology of the Thumbprint Emperor, *Lethrinus harak* (Forsskal, 1775), in Kenyan coastal waters. Western Indian Ocean Journal of Marine Science 1 (2): 135-144

Lachs L, Oñate-Casado J (2020) Fisheries and tourism: social, economic, and ecological trade-offs in coral reef systems. In: Jungblut S, Liebich V, Bode-Dalby M (eds) Youmares 9 - The Oceans: our research, our future: Proceedings of the 2018 conference for young marine researchers, Oldenburg, Germany. Springer International Publishing, Cham. pp. 243-260

Lasi F (2003) Age, growth, mortality rates and reproductive biology of three Fijian emperor fishes (Pisces:Lethrinidae) *Lethrinus harak*. Masters' thesis, University of the South Pacific, Suva, Fiji. 381 pp

Matta ME, and Kimura DK (editors) (2012) Age determination manual of the Alaska Fisheries Science Center, age and growth program. NOAA Professional Paper NMFS 13. 97 pp

Matthews T, Ochavillo D, Felise S, Letalie T, Letuane E, Schuster E, Soonaolo A, Tofaeono S, Tua A, Tuilagi F (2019) Length-weight relationships for 71 reef and bottomfish species from Tutuila and Aunu'u, American Samoa. Pacific Islands Fisheries Science Centre Administrative Report H-19-03. 9 pp

McPherson G, Squire L, O'Brien J (1988) Demersal reef fish project 1984–1985. Age and growth of four important reef fish species. Report to Great Barrier Reef Marine Park Authority, Townsville. 38 pp

Mendoza RPR (2006) Otoliths and their applications in fishery science. Croatian Journal of Fisheries Science 64 (3): 89-102

Midway RS, Ostrowski A, Wes L, Hernandez M, Robertson DM (2018) Improved growth estimates for *Lethrinus harak*: Measuring increments, adjusting ages, and fitting flexible growth models. Fishes 3 (3): 31

Munro JL, Pauly D (2012) A simple method for comparing the growth of fishes and invertebrates. Fishbytes 1: 5-6

Pauly D (1980) On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. ICES Journal of Marine Science 39 (3): 175-192

Pauly D (1984) Fish population dynamics in tropical water: A manual for use with programmable calculator. ICLARM Study and Review 8. International Center for Living Aquatic Resources. Manila, Philipines. 325 pp

Phillips ND, Kubicek L, Payne NL, Harrod C, Eagling LE, Carson CD, Houghton JD (2018) Isometric growth in the world's largest bony fishes (genus *Mola*)? Morphological insights from fisheries bycatch data. Journal of Morphology 279 (9): 1312-1320

Pikitch EK, Rountos KJ, Essington TE (2014) The global contribution of forage fish to marine fisheries and ecosystems. Fish and Fisheries 15: 43-64

Pilling GM, Grandcourt EM, Kirkwood GP (2003) The utility of otolith weight as a predictor of age in the emperor *Lethrinus mahsena* and other tropical fish species. Fisheries Research 60: 493-506

Putnis I, Korņilovs G (2008) Based on ICES, 2008. Report of the workshop on age reading of *Baltic Herring* (WKARBH) 9–13. Riga, Latvia. 39 pp

R Core Team (2020) R A language and environment for statistical computing. R foundation for statistical computing. Vienna, Austria [https://www.R-project.org]

Trianni MS (2016) Life history characteristics and stock status of the thumbprint emperor (*Lethrinus harak*) in Saipan Lagoon. Fisheries Bulletion 114 (4): 409-425

Vasanthrajan M, Jawahar P, Francis T, Venkatasamy M, Kumar SS (2012) Age, growth and mortality characteristics of *Lethrinus nebulosus* (Forsskal, 1775) in Thoothukudi Coast of Tamilnadu, India. SKUAST Journal of Research 13: 6-13

Vieira AR (2023) Assessment of age and growth in fishes. Fishes 8 (10): 479

Wilkinson C (2008) Status of coral reefs of the world. Global Coral Reef Monitoring Network. Reef and Rainforest Research Centre. Townsville, Australia. 152pp