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**COMPARISON OF POPULATION PARAMETERS
OF THE INDIAN OIL SARDINE *SARDINELLA LONGICEPS*
FROM THE MUSCAT REGION (SULTANATE OF OMAN) IN 1997 AND 2020–2021**

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The Indian oil sardine *Sardinella longiceps* plays a key role in the coastal ecosystem of Oman and its fisheries. Total sardine landings along the Omani coast have increased dramatically: from approximately 17,000 t in 1997 to 440,000 t in 2021. A comparison of *S. longiceps* size structure, length–weight relationship, maturity, spawning seasons, growth, mortality parameters, and some stock characteristics in 1997 and in 2020–2021, as well as data obtained during earlier studies in Oman, shows that the biological structure of the population has been relatively stable over the time. The exploitation rate was higher than 0.5, and although the Indian oil sardine can sustain high exploitation rates, its stock in the Omani waters was overexploited. The biological data acquired during the present study provide a basis for management of the fishery; however, monitoring of catches should be continued, so that a longer time series of biological information can be collected and analyzed.

Keywords: Indian oil sardine, *Sardinella longiceps*, length composition, reproductive characteristics, growth, mortality, stock, long-term changes, Muscat, Sea of Oman

Fisheries play a vital role in coastal communities contributing significantly to employment, food security, nutrition, and national economy of the Sultanate of Oman. According to fisheries statistics of FAO [2024], the total fish catches in Oman rose from about 118,600 metric tons (t) in 1994 to 922,000 t in 2021 (Fig. 1A). This remarkable growth was mainly due to increased catches of sardines by almost 27 times, from 14,100 t in 2008 to 376,000 t in 2021, in two regions, Al Wusta and Al Sharqiyah [Fisheries Statistics Book, 2013, 2022]. In other regions, the changes of the sardine landings were not as noticeable. For example, in the Muscat region, the mean landing of sardines during 1994–2011 was around 10,000 t and decreased to only 3,200 t during 2012–2022 [Fisheries Statistics Book, 2003, 2013, 2022] (Fig. 1B). Overall, sardine landings contributed to about 24% of total fishery production in Oman in 1994–2011, and their share increased to approximately 50% in 2018–2021. Recently, the total sardine landing in Oman has dropped significantly, from 440,156 t in 2021 to 280,623 t in 2022. In the Muscat region, the landing has also decreased, from 5,404 t to 3,906 t during these years.

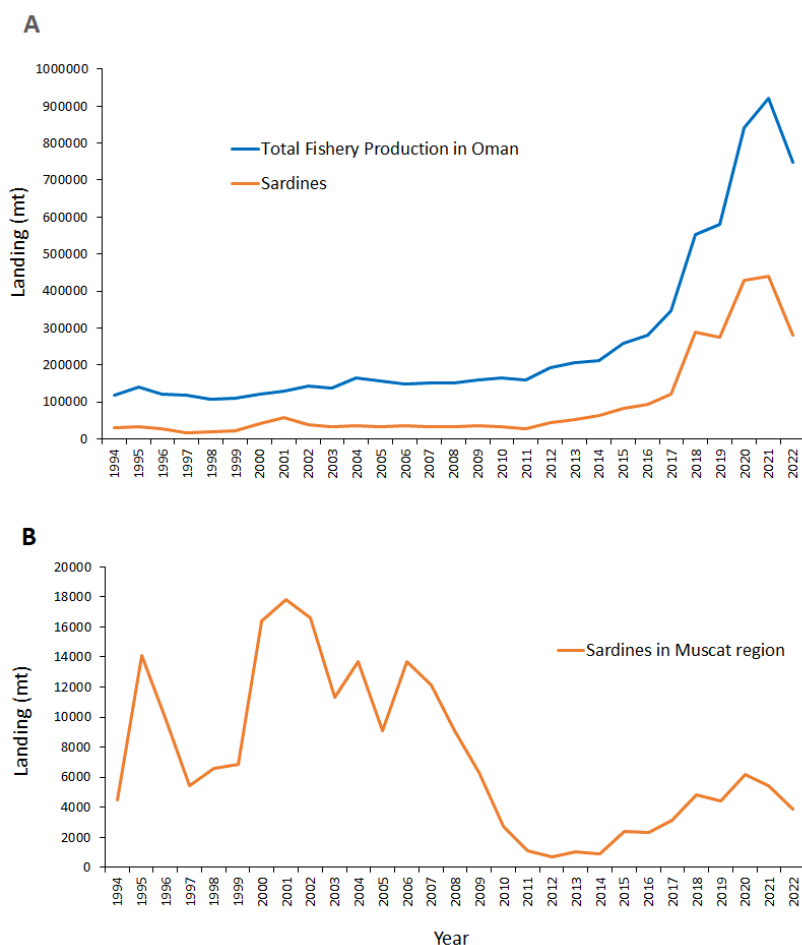


Fig. 1. Total fishery production and sardine landings in Oman (A) and total catches of sardines in the Muscat region (B) in 1994–2022

Five species of sardines (*Sardinella albella*, *S. gibbosa*, *S. longiceps*, *S. melanura*, and *S. sindensis*) are reported from the Omani waters [FishBase, 2024; Randall, 1995]. However, in addition to these species, the blue stripe herring (*Herklotsichthys quadrimaculatus*) and gizzard shad (*Nematalosa nasus*) have been included in the statistics of sardine landings in Oman in recent years [Fisheries Statistics Book, 2013, 2020, 2022]. According to [Al Jufaili, 2021; Al-Abdessalaam, 1995; Zaki et al., 2021], the Indian oil sardine *Sardinella longiceps* Valenciennes, 1847 contributes to about 80% of the total sardine catches in Oman; therefore, this species is of particular interest.

The biology of the Indian oil sardine from different areas of Oman was first studied by M. Al-Barwani et al. [1989]. Research by J. Shaklee and M. Shaklee [1990] suggested the presence of a unit stock of *S. longiceps* in the Omani waters. Different aspects of the reproduction biology of this species have been described by M. Siddeek et al. [1994], S. Al Jufaili [2011] S. Al Jufaili et al. [2006], I. Al-Anbouri et al. [2013], and S. Zaki et al. [2021]. A comprehensive study on the fishery, biology, and stock assessment of the Indian oil sardine was undertaken along the Omani coast during 2007–2009 under the “Small Pelagic Fisheries Project” [Zaki et al., 2011]. Age, growth, mortality, and some stock parameters have been investigated in various regions of Oman, including Muscat [Al-Anbouri et al., 2011; Zaki et al., 2011], Salalah [Zaki et al., 2011, 2013a], Sohar [Zaki et al., 2011, 2013b], and Mahout [Jaya-balan et al., 2014; Zaki et al., 2011]. Several articles were published on *S. longiceps* fishery in Oman,

inter alia those covering studies on gillnet selectivity [Govender, Al-Oufi, 2020], factors driving seasonal and interannual fluctuations of sardine catches [Al Jufaili, Piontkovski, 2020; Piontkovski et al., 2014], and changes in sardine landings along different regions of the Omani coast in 1995–2020 [Al Jufaili, 2021]. Recently, S. Dutta *et al.* [2021; 2024] estimated some population parameters of *S. longiceps* based on samples from the Muscat region in 1997 and between 2004 and 2009. The research of S. Dutta *et al.* [2024] showed that the stock of the species was largely overexploited during these years, with the exception of 2007. Dramatic fluctuations in the Indian oil sardine catches not only lead to changes in income from its fishery, but also affect other valuable marine species, because the sardine is the primary food source for a variety of large pelagic fish, marine mammals, and birds.

The main aim of the study was to compare population parameters of *Sardinella longiceps* in the Muscat region between 1997 and 2020–2021 to determine whether there have been any changes in the biological structure of its assumed single unit stock due to an increase in its total catch in Oman by almost 27 times, although this rise occurred in other areas.

MATERIAL AND METHODS

S. longiceps was sampled randomly in Seeb fish market (the Muscat region) on a monthly basis January to December 1997 (1,375 specimens) and during the period October 2020 to August 2021, except July (394 specimens). The fish were caught by traditional artisanal fishermen using gillnets, surrounding nets, and cast nets. The fish were transferred to the laboratory of the Sultan Qaboos University and measured in total length (TL) to the nearest 1 mm. The total weight (W) and gonad weight (GW) were recorded to the nearest 0.01 g using an electronic balance (Mettler PE 360). Sex and stage of gonad maturity were identified by visual observation of gonads using the five maturity stages scale based on size and color appearance of gonads [Al-Anbouri et al., 2011; Fisheries Techniques, 1995].

The length–weight relationship was estimated using the allometric formula [Le Cren, 1951]:

$$W = a \times L^b, \quad (1)$$

where W is the total wet weight (g);

L is the total length (cm);

a and b are the constants.

The values of the constants a and b were estimated by the least-square linear regression from the logarithmic transformation values of length and weight:

$$\log W = \log a + b \log L, \quad (2)$$

where b is the slope;

log a is the intercept [Zar, 1999].

The regression analysis was conducted using the Regression Analysis tool in MS Office Excel. The 95% confidence limits (CL) of parameters a and b and coefficient of determination (Pearson r^2) were estimated. The coefficient of determination was used as an indicator of the linear regression quality. Regressions were calculated for males, females, and both sexes combined. Analysis of covariance (ANCOVA) was used to find out the significant difference, if any, between relationships of males and females at the 5% level [Snedecor, Cochran, 1989]. The data on length and weight were log transformed in PAST 4.14 [Hammer et al., 2001], and one-way ANCOVA was used to calculate the *p*-value.

The length at first capture (L_c) at which 50% of fish is vulnerable for the given fishing gear was defined by calculating cumulative percentage of fish in 1-cm size classes and applying logistic function [King, 2007]:

$$P = 1/(1 + e^{-a(L-L_c)}) , \quad (3)$$

where P is the proportion of fish in 1-cm length classes;

L is the mid-class length;

L_c is the length at first capture;

a is the constant.

The non-linear least-squares fitting with MS Office Excel Solver was used to obtain the best fit of two parameters, L_c and a.

The same method was applied to calculate the length at first maturity (L_m). Females with ovaries and males with testis in stages 3, 4, and 5 were considered sexually mature. The cumulative percentage occurrence of mature fish of both sexes in 1-cm size groups for the studied years was determined; the logistic function (formula 3) and the non-linear least-squares fitting with MS Office Excel Solver were used to obtain L_m .

The sex ratio was determined as a number of males to number of females (M : F). The monthly sex ratios were tested for significant deviations from the expected ratio with Pearson's chi-square (χ^2) goodness-of-fit test [Snedecor, Cochran, 1989] using the formula:

$$\chi^2 = \sum (O - E)^2 / E , \quad (4)$$

where O is observed numbers;

E is expected numbers.

The p -value was calculated applying CHISQ.TEST function in MS Office Excel.

To determine the spawning season, percentage occurrence of different maturity stages of gonads during various months was calculated and plotted separately for males and females together with the gonadosomatic index (hereinafter GSI). Stages 1 and 2 were considered immature and inactive; stage 3, developing/ripening; stage 4, ripe; and stage 5, running/spawning. GSI was established using the formula of R. Wydoski and E. Cooper [1966]:

$$GSI = GW/W \times 100 , \quad (5)$$

where GW is the gonad weight (g);

W is the total weight (g).

No clear annual growth rings were found in *S. longiceps* scales and otoliths, or they were highly inconsistent [Abdussamad et al., 2023; Al-Barwani, Prabhakar, 1989; Zaki et al., 2011]; hence, calculated length-based method was applied for age and growth estimations in the present study. To determine growth parameters in von Bertalanffy growth function (hereinafter VBGF), the Electronic Length Frequency Analysis (ELEFAN) with nonseasonal growth was used; this technique is incorporated in Tropical Fisheries Analysis (TropFishR) package [Mildenberger et al., 2017].

The age at first maturity at which fish of a given population mature for the first time was calculated from the length at first maturity using the inverse of VBGF [Mackay, Moreau, 1990]:

$$T_m = t_o - \ln(1 - L_m/L_\infty)/K , \quad (6)$$

where T_m is age at first maturity;

t_o is the age in VBGF;

L_∞ is the asymptotic length;

L_m is the length at first maturity;

K is the growth coefficient.

The potential life span (longevity) was determined by the formula of C. Taylor [1958] which is based on the estimated parameters of VBGF:

$$T_{max} = t_o + 3/K , \quad (7)$$

where t_o is the hypothetical age;

K is instantaneous growth coefficient in VBGF.

The optimal fishing length (L_{opt}), the length at which the unfished cohort provides the maximum possible yield, was estimated from the equation given by R. Beverton [1992]:

$$L_{opt} = L_{\infty}(3/(3 + M/K)) , \quad (8)$$

where L_{∞} and K are parameters of VBGF;

M is the natural mortality.

The annual instantaneous rate of natural mortality (M) was estimated in TropFishR by the empirical equation of A. Then *et al.* [2015]:

$$M = 4.118K^{0.73}L_{\infty}^{-0.33} , \quad (9)$$

where L_{∞} (cm) is the von Bertalanffy coefficient.

The length converted catch curve method incorporated in TropFishR was employed for the calculation of total mortality coefficient (Z).

The fishing mortality (F) was determined as follows: $F = Z - M$.

The exploitation rate (E), or the fraction of deaths caused by fishing [Gulland, 1971; Ricker, 1975; Sparre, Venema, 1998], was computed as:

$$E = F/Z . \quad (10)$$

The exploitation ratio (U), as a fraction of the fish caught during the year, was obtained from the equation given by W. Ricker [1975]:

$$U = F/Z(1 - e^{-Z}) . \quad (11)$$

The annual landing (in tons) in the present study was considered as the yield (Y).

The total stock (P) in weight was estimated from the ratio [Amin *et al.*, 2002]:

$$P = Y/U , \quad (12)$$

where Y is the annual average yield of the species (t);

U is the exploitation ratio.

The term standing stock biomass (B) refers to the concentration of fish populations in a given area at a given time. This can be estimated in terms of numbers or weight. In the present study, the standing stock was determined by weight using the formula [Amin *et al.*, 2002]:

$$B = Y/F , \quad (13)$$

where Y is the annual yield (t);

F is the fishing mortality.

The maximum sustainable yield (hereinafter MSY) was calculated by the equation suggested by E. Cadima [Sparre, Venema, 1998; Troadec, 1977]:

$$MSY = 0.5(Y + M \times B) , \quad (14)$$

where Y is the total landing in a year;

M is the natural mortality;

B is the standing stock biomass in that same year.

Statistical analysis was performed using MS Office Excel and PAST 4.14 [Hammer et al., 2001].

RESULTS

Size composition. The total length of the Indian oil sardine in the studied samples in 1997 ranged between 10.0 and 21.3 cm [mean was (16.26 ± 2.04) cm], and weight ranged between 8.2 and 91.0 g [mean was (38.66 ± 14.91) g]. Females were slightly smaller than males; the mean length of females was (16.06 ± 2.14) cm, and that of males was (16.59 ± 1.81) cm. Student's *t*-test and Kolmogorov–Smirnov two-sample test showed significant differences between means and length frequency distributions of females and males ($p < 0.001$).

In the samples of 2020–2021, the total length of *S. longiceps* varied between 9.7 and 20.9 cm [mean was (16.26 ± 2.20) cm], and weight varied between 7.3 and 77.6 g [mean was (39.71 ± 14.88) g]. In contrast to the case of 1997, females were slightly larger than males; their mean length was (16.45 ± 2.30) cm, and that of males was (16.05 ± 2.03) cm. Differences between total length means and length distributions of males and females were non-significant in this case.

Comparisons between 1997 and 2020–2021 showed no significant differences in the mean length and length frequency distribution of *S. longiceps* (*t*-test, $p = 0.978$; Kolmogorov–Smirnov test, $p = 0.09$). Fish less than 14 cm contributed to about 5–6% of the catch in 1997 and 2021–2022, while the largest specimens, more than 20 cm, 10–11%. The length frequency distribution indicates three distinct modes in both cases: 13.5–14.0, 16.5–17.0, and 19.5–20.0 cm for 1997 and 14.5–15, 17.0–17.5, and 19.5–20.0 cm for 2020–2021 (Fig. 2).

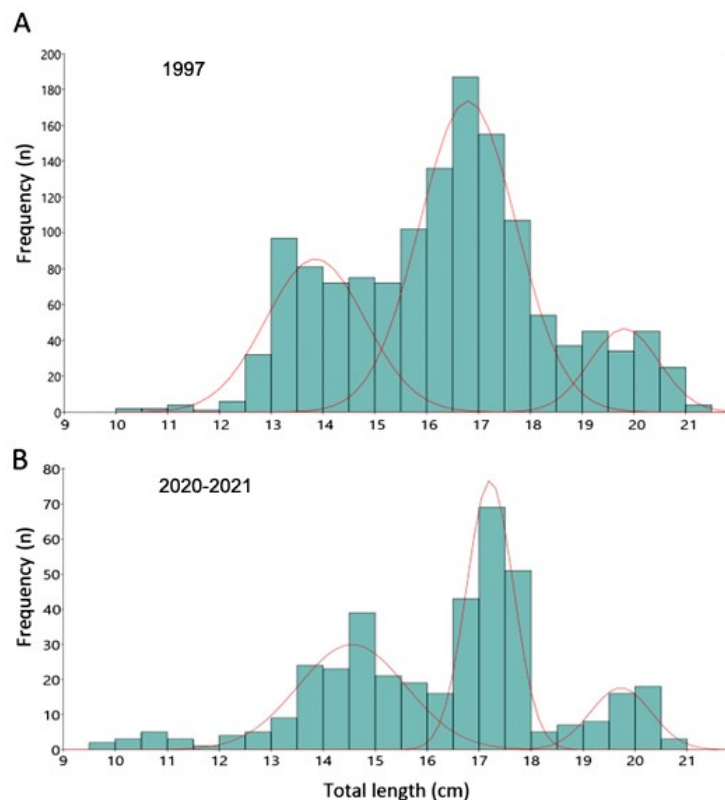


Fig. 2. Length frequency distribution of *Sardinella longiceps* from commercial catches in the Muscat region in 1997 (A) and 2020–2021 (B)

Monthly fluctuations of the mean length were very similar during 1997 and in 2020–2021 combined by months in one year (Fig. 3). Larger specimens were observed in winter time (December to February), while smaller sardines occurred mostly during summer and autumn (June to October).

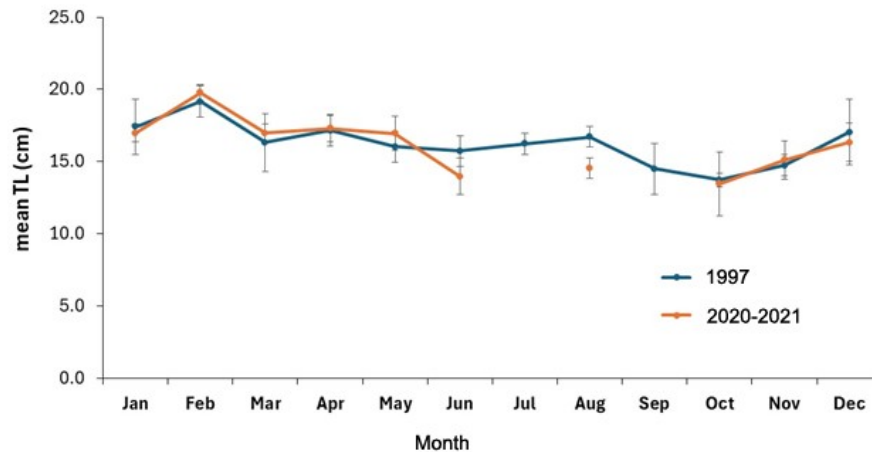


Fig. 3. Monthly fluctuations of the mean total length (TL) of *Sardinella longiceps* from the Muscat region in 1997 and 2020–2021

Length–weight relationship. Parameters a and b in the relationship between somatic weight and total length of *S. longiceps* for both sexes combined in 1997 and 2020–2022 (formula 2) were very similar (Table 1). The value of parameter b was estimated in 3.01 and 3.05, respectively, indicating a close to isometric growth in weight for the species. The coefficient of determination (r^2) was very high in both cases ranging 0.96–0.97. ANCOVA test showed no significant difference between the slopes of the length–weight relationship in 1997 and 2020–2021 ($p > 0.05$).

Table 1. Length–weight relationship of *Sardinella longiceps* from the Muscat region in 1997 and 2020–2021 (CL, confidence limits)

Years	n	a	95% CL a	b	95% CL b	r^2
1997	1,375	0.0083	0.0077–0.0089	3.0114	2.9871–3.0368	0.970
2020–2021	394	0.0076	0.0064–0.0090	3.0494	3.9867–3.1127	0.955

Length at first capture. The mean length at which 50% of fish were caught (L_c) (formula 3) was estimated to be 16.20 cm for 1997 and 16.28 cm for 2020–2021 (Fig. 4).

Length and age at first maturity. During 1997, the smallest male with ripening testis (stage 3) was 13.2 cm, and the smallest female with ripening ovary (stage 3) was 13.5 cm, while in 2020–2021, the sizes were 13.5 and 13.6 cm, respectively. Maturing testis (stage 3 and above) and maturing ovaries (stage 3 and above) were used for determination of the length at first sexual maturity. The logistic function (formula 3) showed that the mean size at the first maturity (L_m) during 1997 was 17.06 cm in males and 17.36 cm in females; during 2020–2021, it was 16.59 and 17.21 cm, respectively (Fig. 5). The result indicates that males of the Indian oil sardine mature at a slightly earlier length than females.

The age at first maturity (formula 5) was calculated for females at 1.35 years in 1997 and 1.38 years in 2020–2021.

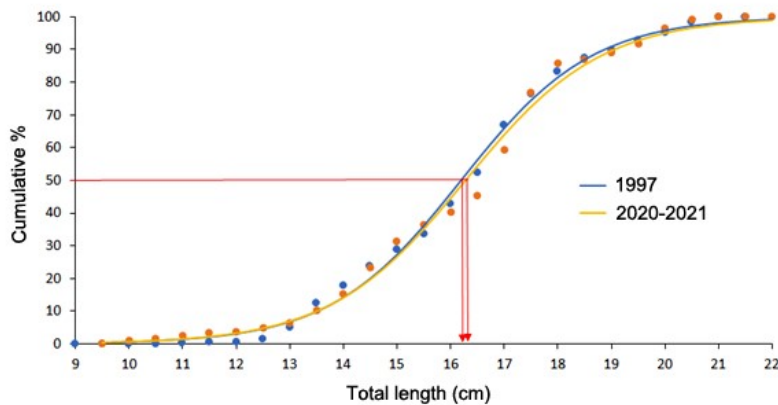


Fig. 4. Curves of cumulative percentages of catches of *Sardinella longiceps* of different sizes in the Muscat region and the length at first capture in 1997 and 2020–2021

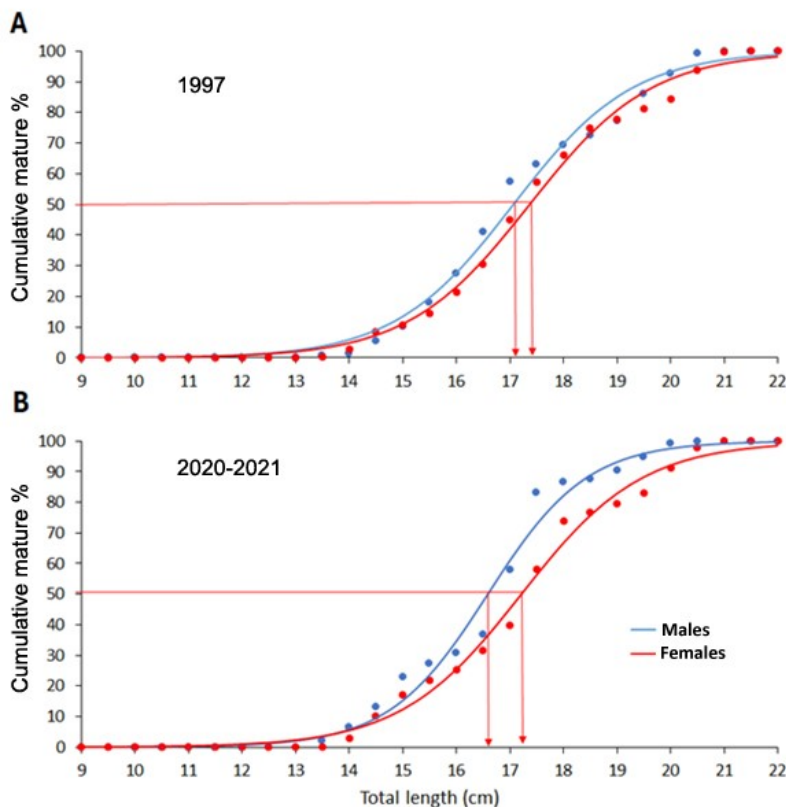


Fig. 5. Curves of cumulative percentage of mature *Sardinella longiceps* and the length at first maturity for males and females from the Muscat region in 1997 (A) and 2020–2021 (B)

Sex ratio. The sex ratio of *S. longiceps* during both studied periods was in favor of females. In 1997, females constituted 62% of the analyzed fish, and M : F = 0.60 : 1. In 2020–2021, the percentage of females was 55%, and M : F = 0.83 : 1.

The investigation of the monthly sex ratio indicated the dominance of females over males during most of the year. Males were absent in the sample from commercial catches in October 1997. The share of males was found to be larger than that of females only in June 1997, November 2021, and April 2021. The chi-square test revealed that the monthly sex ratio was significantly different from what was expected in June, August, and October 1997, while in 2020–2021, only in November. In general, the monthly sex ratio differed significantly during 1997 ($\chi^2 = 46.64$, $p = 0.002$) and non-significantly during the studied months of 2020–2021 ($\chi^2 = 12.47$, $p = 0.65$).

Spawning season. The monthly occurrence of fish with immature, ripening, and spawning gonads during 1997 indicated higher percentages of spawning males and females during November–March, in June, and during August–September. Higher GSI values were calculated for males in February and August and for females in March and August (Fig. 6).

A similar picture was observed during 2020–2021: the fish with ripening and spawning gonads dominated from November to April and in August. Higher GSI values were recorded for males during January–April and in August, and for females, during February–April and in August. Hence, spawning of the Indian oil sardine in the Muscat region may occur between November and April with a peak in March–April and again in June to September with a peak in August.

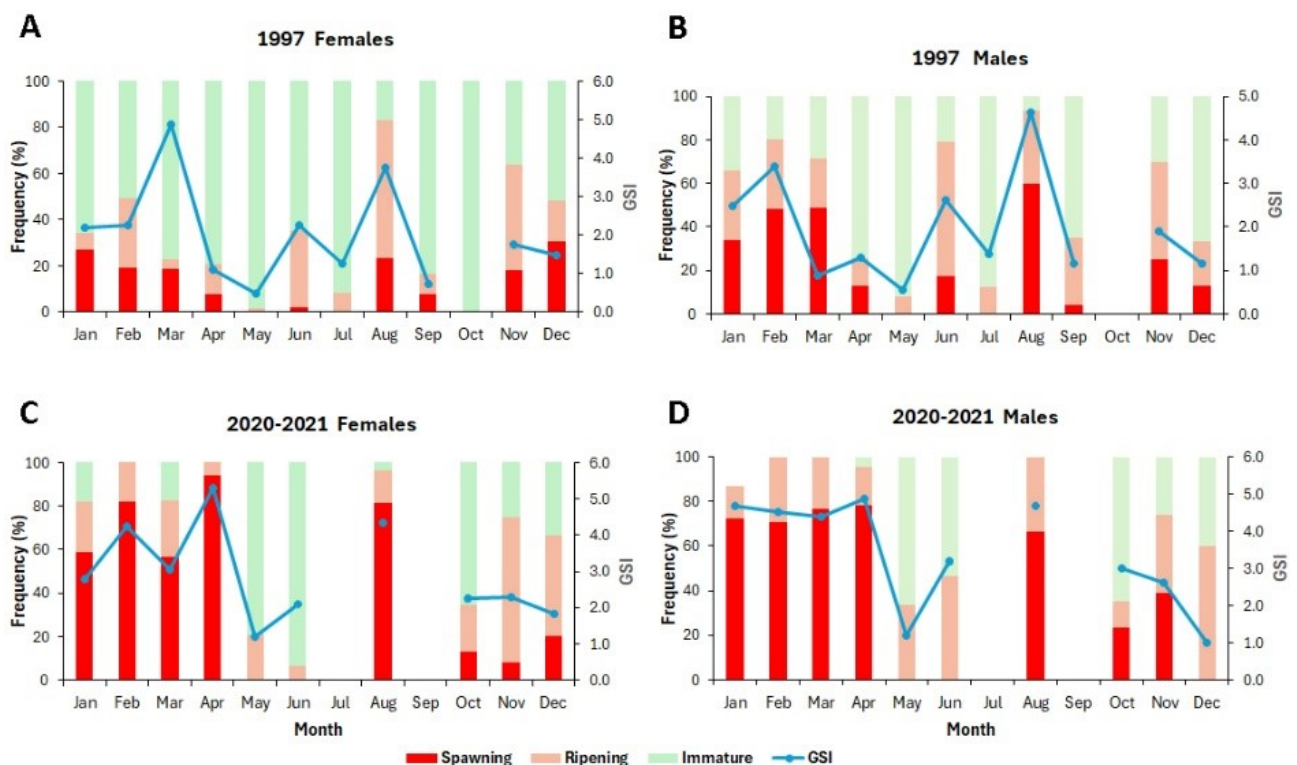


Fig. 6. Monthly changes of different gonad developmental stages (in percentage) and values of the gonadosomatic index (GSI) of *Sardinella longiceps* in the waters of Muscat: A and B, females and males, respectively, in 1997; C and D, females and males, respectively, in 2020–2021

Age, growth, and life span. Growth parameters of *S. longiceps* in VBGF estimated based on the monthly length frequency distributions using ELEFAN technique in TropFishR are provided in Fig. 7 and Table 2. In 1997 and 2020–2021, the asymptotic length (L_{∞}) and growth coefficient (K) were similar. Calculated lengths of one-, two-, and three-year-old fish were 15.7, 18.7–19.0, and 19.6–20.2 cm in 1997 and 2020–2021. Our result showed that *S. longiceps* grows very rapidly during the first year of life; then, its growth slows down, until it becomes almost negligible (after 2.5 years). From Fig. 7, new generations appeared in February 1997 and February 2021.

According to calculation by empirical formula 7, the maximum life span of the studied species was 2.36 years in 1997 and 2.60 in 2020–2021. Commercial catches of the sardine during 1997 comprised mainly one- to two-year-old fish, while in 2020–2021, fish younger by one year.

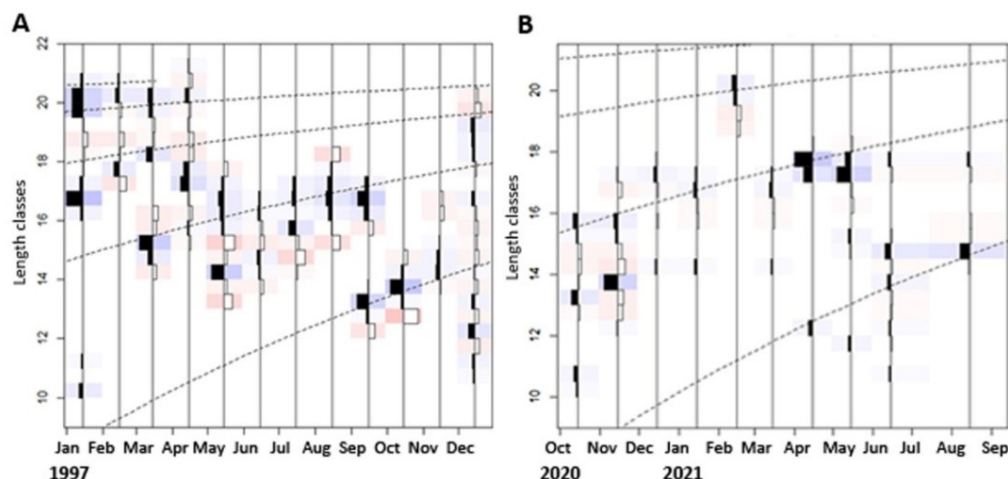


Fig. 7. Monthly length frequency distribution and growth curves for *Sardinella longiceps* from the Muscat region: A, 1997; B, 2020–2021

Table 2. Growth parameters in von Bertalanffy growth function and calculated length at different age for *Sardinella longiceps* from the Muscat region

Years	L_{∞}	K	t_0	Mean TL, cm					
				0.5 years	1 year	1.5 years	2 years	2.5 years	3 years
1997	20.1	1.11	-0.37	12.4	15.7	17.6	18.7	19.3	19.6
2020–2021	20.9	1.00	-0.40	12.4	15.7	17.8	19.0	19.8	20.2

Optimal fishing length. The length at which a year class (cohort) provides the maximum biomass in an unfished population (L_{opt}) was calculated (formula 8) to be 13.37 cm in 1997 and 13.90 cm in 2020–2021.

Mortality. The natural mortality (M) estimated in TropFishR package with the empirical Then's equation (formula 9) was 1.66 yr^{-1} in 1997 and 1.51 yr^{-1} in 2020–2021.

The total mortality (Z) assessed using the length converted catch curve method in TropFishR was 4.29 yr^{-1} ($SE = 0.23$) in 1997 and 4.42 yr^{-1} ($SE = 0.19$) in 2020–2021.

The fishing mortality (F) was estimated at 2.63 yr^{-1} for 1997 and 2.91 yr^{-1} for 2020–2021.

Exploitation rate, biomass, and maximum sustainable yield. *S. longiceps* fishery in the Muscat region was assessed applying several simple formulas. The exploitation rates (E) calculated based on formula 10 were 0.61 in 1997 and 0.66 in 2020–2021, and the exploitation ratios (U) determined from formula 11 were 0.60 and 0.65, respectively (Table 3). Further calculations were carried out separately for total catches of *S. longiceps* in Oman and catches in the Muscat region alone. It was assumed that in both cases, the Indian oil sardine accounted for 80% of the total sardine catches. The landings, or yield (Y), of *S. longiceps* in the Muscat region in 1997 and 2021 were very similar comprising approximately 4.3 thousand tons, while the total oil sardine landings in Oman differed by more than 26 times: from about 13.5 thousand tons in 1997 to 352 thousand tons in 2020–2021. Annual landings in Oman and the Muscat region in 1997 were about 123% of calculated MSY, and in 2021, approximately 132% of MSY. So, the effort for *S. longiceps* fishery in these years was higher than MSY indicating overfishing of the stock.

Table 3. Assessment of stock parameters of *Sardinella longiceps* based on annual landings in the Muscat region and total landings in the waters of Oman in 1997 and 2021 (t, tons)

Year	Region	E	U	Y, t	P, t	B, t	MSY, t
1997	Oman	0.61	0.60	13,412	22,353	5,100	10,939
	Muscat			4,356	7,260	1,656	3,552
2021	Oman	0.66	0.65	352,125	541,731	121,005	267,421
	Muscat			4,324	6,652	1,486	3,284

DISCUSSION

The Indian oil sardine is a small pelagic fish playing a key role in the coastal ecosystem and fisheries of Oman. The sardine landings in Oman have increased almost 27 times in the compared years: from 16,765 t in 1997 to 440,156 t in 2021. However, in the Muscat region, the sardine landings remained relatively stable: 5,445 and 5,405 t, respectively. This sharp gain in catches raises questions about possible overfishing and its effect on the population structure and the sardine stock. It also causes concerns about the future of fishing in Oman and the potential effects on other species in the ecosystem. Therefore, the population parameters of *S. longiceps* in 1997 were compared with those in 2020–2021, as well as with the results of other studies conducted in other years and areas of Oman.

According to our data, the maximum total length of *S. longiceps* was 21.3 cm in 1997 and 20.9 cm in 2020–2021. The mean length of the fish in the compared years was exactly the same (16.26 cm), and the average weight did not differ significantly: 38.66 vs. 39.71 g (Table 4). According to literature data, the maximum total length of *S. longiceps* in the Omani waters has reached 23.0 cm, and the maximum weight, 152.0 g, was recorded in Mahut in 2007–2009 [Zaki et al., 2021]. The mean length of this species in commercial catches in various regions of Oman in 2007–2009 ranged 16.05 to 18.42 cm, and the average weight ranged 37.96 to 57.47 g [Zaki et al., 2011].

The length–weight relationship of *S. longiceps* was similar in 1997 and 2021–2021 ($a = 0.008$; $b = 3.01 \dots 3.05$) that evidences for isometric growth of the species. However, as we know, the body shape and the coefficients a and b depend on many factors, in particular, the fat content and gonad condition, and can vary significantly between seasons and between different years. S. Dutta et al. [2021] found that the parameter b for *S. longiceps* from the Muscat region was < 3 in some years suggesting negative allometric growth, but in other years, it was > 3 indicating positive allometric growth for this species.

We calculated the length at first capture of *S. longiceps* from the Muscat region in 1997 to be 16.20 cm, and in 2020–2021, 16.28 cm. It is quite similar and comparable to the results of S. Zaki et al. [2011; 2013b] but slightly smaller than the length calculated for Mahout region by N. Jayabalan et al. [2014].

The length at first maturity (L_m) for *S. longiceps* males and females ranged 16.6 to 17.4 cm. It has also been found that the fish attain the first maturity at the end or just after the first year of life. Most other studies have also shown that the Indian oil sardine from the Omani coast reaches maturity at about 16–18 cm and at the age of about 1 year [Al Jufaili, 2011; Siddeek et al., 1994; Zaki et al., 2011, 2012]. However, as reported in some papers, this species can mature at a smaller length (12.5–13.5 cm) [Dorr III, 1990] or larger one (18–19 cm) [Al-Anbouri et al., 2013; Zaki et al., 2021]. The age of maturation or rate of sexual maturity of a particular fish species depends on some external factors, and the most important of them are food, temperature, photoperiod, and water currents [Bhukaswan, 1980]. Notably, in most studies, when assessing the size at the first maturity of *S. longiceps* in Oman, it was found that males reach maturity at a slightly smaller length than females.

Table 4. Comparison of data on sizes, parameters of length–weight relationship (LWR), length at first capture (L_c), length at first maturity (L_m), and spawning seasons for *Sardinella longiceps* in different regions of Oman (M, male; F, female)

Years	Region	Mean TL, cm	Maximum TL, cm	Mean W, g	Maximum W, g	LWR		L_c , cm	L_m , cm	Spawning season, months	Reference
						a	b				
–	Muscat	–	–	–	–	–	–	–	12.5–13.5	Sep–Feb, Mar–Apr	Dorr III, 1990
–	Muscat	–	–	–	–	–	–	–	15.9	Apr, Oct	Siddeek et al., 1994
1997–1998	Muscat	16.47 M, 16.60 F	21.9	–	–	0.0081	3.0	–	16.7 M, 16.9 F	Feb, Mar, Aug	Al Jufaili, 2011
2005	Muscat	–	–	–	–	–	–	–	–	Mar–Apr, Aug	Al Jufaili et al., 2006
1997	Muscat	16.19	21.3	38.24	91.00	0.0063	3.0	–	–	–	Dutta et al., 2021
2004	Muscat	16.71	22.0	44.50	94.60	0.0043	3.18	–	–	–	
2005	Muscat	16.05	18.2	37.96	58.40	0.0097	2.81	–	–	–	
2006	Muscat	18.42	21.1	57.47	89.70	0.011	2.76	–	–	–	
2007	Muscat	16.34	22.0	39.58	83.60	0.0087	2.85	–	–	–	
2009	Muscat	17.76	22.0	52.34	108.00	0.0036	3.25	–	–	–	
2008–2009	Muscat	–	20.0	–	–	–	–	–	18.2	Dec–Mar, Jun–Sep	Al-Anbouri et al., 2013
2007–2009	Muscat	–	22.0	–	–	0.005	3.09	16.9	16.2–17.4 M, 16.4–17.6 F	Jan–Apr, Jun–Sep	Zaki et al., 2011
2007–2009	Mahout	–	22.8	–	–	0.001	2.91	19.3	–	–	Jayabalan et al., 2014
2007–2009	Mahout	–	23.0	–	152.0	–	–	–	18.7 M, 19.1 F	Jan–Feb, Jul–Sep	Zaki et al., 2021
2007–2009	Salalah	–	21.0	–	–	0.007	3.03	18.5	–	–	Zaki et al., 2013a
2007–2009	Sohar	–	–	–	–	–	–	–	15.6 M, 16.3 F	Feb–Mar, Sep–Oct	Zaki et al., 2012
2007–2009	Sohar	–	21.0	–	–	0.004	2.70	16.8	17.8–18.2 M, 18.2–18.4 F	Mar–Jul	Zaki et al., 2013b
1997	Muscat	16.26	21.3	38.66	91.0	0.0083	3.01	16.2	17.1 M, 17.4 F	Mar–Apr, Jun–Sep	present study
2020–2021	Muscat	16.26	20.9	39.71	77.6	0.0076	3.05	16.3	16.6 M, 17.2 F	Feb–Apr, Aug	present study

Our analysis of monthly fluctuations in occurrence of various gonad stages of males and females showed that there were ripening and spawning sardines in almost all the studied months, except for May and October 1997. This indicates that the Indian oil sardine spawns, as a rule, all year round; however, the spawning activity varies greatly throughout the year. The higher percentage of ripe and spawning fish (stages 4 and 5) was observed in January–April, August, and November–December both during 1997 and in 2020–2021. Higher GSI values were obtained in February–March and August 1997, as well as in April and August 2021. Thus, two peaks of spawning activity were detected: the first one, in February–April, and the second one, in August. This result is consistent with other investigations that also reported two spawning seasons of *S. longiceps* in the Omani waters (see Table 4). In particular, in the Muscat region, the first spawning season was observed December to April, and the second, June to October [Al Jufaili, 2011; Al Jufaili et al., 2006; Al-Anbouri et al., 2013; Siddeek et al., 1994; Zaki et al., 2011]. The spawning season of *S. longiceps* depends on environmental conditions in the sea and might vary from year to year and from region to region in Oman [Al Jufaili et al., 2006; Siddeek et al., 1994].

The sex ratio of *S. longiceps* was in favor of females – 0.60 : 1 (38% males and 62% females) in 1997 and 0.83 : 1 (45% males and 55% females) in 2020–2021 – demonstrating a significant deviation from the expected ratio of 1 : 1 ($p < 0.01$). This is consistent with the studies of S. Al Jufaili et al. [2011] and S. Zaki et al. [2011; 2012; 2021] which also showed the dominance of *S. longiceps* females over males in all analyzed regions – Muscat, Mahout, Salalah, and Sohar – in 1997–1998 and 2007–2009. Combining our material with literature data [Zaki et al., 2011] on abundance of males and females, we concluded that the Indian oil sardine has an overall female-biased sex ratio 0.64 : 1 (39% males and 61% females) in the Omani waters. This pattern means increasing egg production *per* population biomass for the species. The sex ratio provides basic information for assessing the reproductive potential and estimating stock size of fish populations. There is a wide variation in sex determination systems in fish, where sex can be determined by environmental factors (mainly temperature) and genetic ones [Baroiller et al., 2009; Conover, Heins, 1987]. In this case with *S. longiceps*, the sex ratio seems to be determined primarily by genetic factors.

S. longiceps age and growth are difficult to establish by studying otoliths and other hard parts (scales and vertebrae), as there are no clear annual rings [Al-Barwani, Prabhakar, 1989; Zaki et al., 2011]. However, some attempts were made in early works to analyze the age of sardines [Balan, 1964; Hornell, Naidu, 1924; Nair, 1949, 1952]. These investigations have shown that the Indian oil sardine has a rapid growth rate and a life span of about three years, and the fish reach sexual maturity at about 15 cm in length at the age of one year [Hornell, Naidu, 1924] or two years [Nair, 1952]. Recently, age and growth of *S. longiceps* from Indian waters were assessed by three approaches: interpretation of microstructures on hard parts (mainly otoliths), modal progression analysis of length frequency data of fish caught in commercial fishing, and direct measurement of sardines reared in open sea cages on natural food during 11 months [Abdussamad et al., 2023]. The authors reported a much faster growth rate (K of 1.57 and 1.76 yr^{-1}) for this species compared to values in previous investigations. However, they also found a significant difference in the sardine growth rate between different years, when, according to their results, one-year-old fish reached 20.4 cm in 2011–2013 and only 15.6 cm in 2014–2017.

Studies on *S. longiceps* age and growth in the Omani waters are largely based on length frequency analysis [Al-Anbouri et al., 2011; Dutta et al., 2024; Jayabalan et al., 2014; Zaki et al., 2011, 2013a, b, 2021] which was also used in the present research. Overall, our data showed similar growth parameters for the sardine in 1997 and 2020–2021. When comparing our results with those of other investigations, it can be noted that we obtained lower L_{∞} values, except for values in the work of M. Siddeek et al. [1994],

but K values are similar to those in most previous works (Table 5). Some differences in growth parameters with the results of other authors may be related to calculation procedures, as we used ELEFAN from TropFishR package, while S. Zaki *et al.* [2011; 2013a; 2013b; 2021] and N. Jayabalan *et al.* [2014] applied ELEFAN routine incorporated in LFDA5 of Fish Stock Assessment Software (FMSP) developed by MRAG Ltd [Kirkwood *et al.*, 2003], and S. Dutta *et al.* [2024] calculated L_{∞} and K values using ELEFAN I from FiSAT II [Gayanilo *et al.*, 2005]. However, in general, all the results on *S. longiceps* growth and life span presented in Table 5 are comparable, and the observed differences may be due to variations in growth rate in different years and regions which depend on environmental conditions and food availability, but have no clear relationship with fishing intensity.

Table 5. Summary of *Sardinella longiceps* growth parameters, mortality, and exploitation rate in the waters of Oman

Years	Region	L_{∞} , cm	K , yr^{-1}	t_0 , yr	$T_{\max}$, yr	Z , yr^{-1}	M , yr^{-1}	F , yr^{-1}	E	Reference
–	Muscat	19.72	0.986	–	3.75	–	–	–	–	Siddeek <i>et al.</i> , 1994
2008–2009	Muscat	22.02	1.21	–0.01	2.5	4.11	2.21	1.91	0.46	Al-Anbouri <i>et al.</i> , 2011
2007–2009	Muscat	23.18	1.21	–0.21	2.0	4.17	2.22	1.99	0.47	Zaki <i>et al.</i> , 2011
2007–2009	Mahout	23.00	1.33	–0.09	2.5	3.66	2.21	1.45	0.40	Jayabalan <i>et al.</i> , 2014
2007–2009	Salalah	23.02	1.57	–0.49	2.0	4.65	2.45	2.20	0.47	Zaki <i>et al.</i> , 2013a
2007–2009	Sohar	23.00	1.40	–0.15	2.5	3.97	2.28	1.69	0.43	Zaki <i>et al.</i> , 2013b
1997	Muscat	22.80	1.10	–0.08	2.64	4.69	1.08	3.61	0.77	Dutta <i>et al.</i> , 2024
2004	Muscat	23.63	1.20	–0.07	2.43	4.50	1.13	3.37	0.75	
2007	Muscat	23.42	1.0	–0.09	2.91	1.89	1.01	0.88	0.47	
2009	Muscat	23.42	0.94	–0.10	3.10	6.30	0.97	5.33	0.85	
1997	Muscat	20.1	1.11	–0.37	2.36	4.29	1.65	2.63	0.61	present study
2020–2021	Muscat	20.9	1.10	–0.40	2.60	4.42	1.51	2.91	0.66	present study

The Indian oil sardine has a high rate of natural mortality (M) previously estimated based on the empirical equation of D. Pauly [1980]: 2.21 to 2.45 yr^{-1} [Al-Anbouri *et al.*, 2011; Jayabalan *et al.*, 2014; Zaki *et al.*, 2011, 2013a, b, 2021]. However, according to S. Dutta *et al.* [2024], it ranged between 0.97 and 1.13 yr^{-1} (see Table 5). In fact, natural mortality is very difficult to determine, but this parameter is pretty important in most stock assessments. Many methods have been developed to predict natural mortality, and one of the most popular is Pauly's empirical formula based on growth parameters and water temperature [Pauly, 1980]. Recently A. Then *et al.* [2015] proposed new formulas for estimating natural mortality using data from 200 fish species; those are based on maximum age ($t_{\max}$) or asymptotic length (L_{∞}). This method is included in TropFishR package; therefore, we used it and calculated *S. longiceps* natural mortality at 1.65 yr^{-1} for 1997 and 1.51 yr^{-1} for 2020–2021. In the case of applying Pauly's formula, the coefficient M was estimated at 2.15 and 2.11 yr^{-1} , respectively.

Our estimates of the total mortality (Z) were similar to those for the years studied and to results of most other authors [Al-Anbouri *et al.*, 2011; Jayabalan *et al.*, 2014; Zaki *et al.*, 2011, 2013a, b, 2021]. It can be noted that Z estimates of S. Dutta *et al.* [2024] varied greatly, and for 2007 and 2009, they differed significantly from other results. With the chosen approach, values of natural and total mortalities determine further calculations of fish population parameters, such as fishing mortality, exploitation rate, and, together with catch data, also total stock, standing stock, and MSY. So, the exploitation rate (E) was > 0.5 in the case of using estimates of M according to Then's formula and close to 0.5 if we applied the Pauly's formula.

Previous studies have shown that *S. longiceps* landings in different regions of Oman in some years within 1997–2009 were either lower or close to the optimal level [Al-Anbouri et al., 2011; Jayabalan et al., 2014; Zaki et al., 2011, 2013a, b]. On the other hand, S. Dutta et al. [2024] reported that the stock of the species was largely overexploited in this time. From our results, *S. longiceps* stock was overexploited in 1997, as well as in 2020–2021. J. Gulland [1983] recommends 0.5 as a suitable exploitation rate for fish stocks in temperate water. However, fish forming stocks in tropical and subtropical areas are characterized by short life cycles and rapid growth, and they can sustain high exploitation rates [Wang et al., 2012].

Conclusion. Our results on biological and population parameters of *Sardinella longiceps* for 1997 and 2020–2021, as well as their comparison with results of similar investigations in other years, indicate that its life-history and population parameters have not changed significantly because of a sharp increase in the sardine fishing along the Omani coast in recent years. The present study is based on data from the Muscat region of the Sea of Oman, where sardine catches were almost identical in compared years, while a sharp rise in the sardine catches occurred in the southern regions of the country, Al Wusta and Al Sharqiyah, located in the Arabian Sea. Many investigations have shown that population parameters of *S. longiceps* vary noticeably in different areas and in different years. It is necessary to analyze the structure of stocks of the Indian oil sardine along the Omani coast applying modern genetic techniques.

It would be more appropriate to use otoliths for determining *S. longiceps* age. Data generated from otolith study would aid in better eco-biological understanding of the species, in establishing precise time of birth, and in identifying cohorts that support the fishery and possible interregional migration of this fish. The sardine stock biomass and landings have been highly variable in the long-time series. The present approximate estimations based on growth, mortality, and landing data do not provide true dynamics of the sardine stock; so, it is necessary to apply integrated analytical models that include catch-at-age data, catch-per-unit effort, and stock-recruitment model together with direct assessment methods, such as acoustic, trawling, and aerial survey, as well as egg and larvae surveys. The use of direct and indirect methods can help to improve the accuracy and reliability of the sardine stock assessments, and it is essential for the fishery management and development of the fishery sector.

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СРАВНЕНИЕ ПОПУЛЯЦИОННЫХ ПАРАМЕТРОВ ЖИРНОЙ ИНДИЙСКОЙ САРДИНЫ *SARDINELLA LONGICEPS* ИЗ РАЙОНА МАСКАТА (СУЛТАНАТ ОМАН) В 1997 И 2020–2021 ГГ.

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Жирная индийская сардина *Sardinella longiceps* играет ключевую роль в прибрежной экосистеме и в рыболовстве Омана. Общий объём вылова сардин вдоль побережья Омана резко возрос — примерно с 17 000 т в 1997 г. до 440 000 т в 2021 г. Сравнение размерной структуры, соотношения длины и массы тела, динамики зрелости, периодов нереста, показателей роста, смертности и некоторых популяционных характеристик *S. longiceps* из района Маската в 1997 и 2020–2021 гг., а также сопоставление данных, полученных в ходе более ранних исследований в Омане, демонстрирует, что биологическая структура популяции в исследуемые годы была относительно стабильной. Уровень эксплуатации запаса в то время превышал 0,5, то есть запас *S. longiceps* в водах Омана подвергался чрезмерной эксплуатации (при этом известно, что сардина способна выдерживать высокие уровни). Биологические данные, полученные в ходе настоящей работы, могут служить основой для управления промыслом этого вида, однако необходимо продолжать мониторинг уловов, чтобы собирать и анализировать более длительные временные ряды биологической информации.

Ключевые слова: жирная индийская сардина, *Sardinella longiceps*, размерный состав, репродуктивные характеристики, рост, смертность, запас, многолетняя изменчивость, Маскат, Оманский залив