Population parameters and stock status of skipjack tuna *Katsuwonus pelamis* (Linnaeus, 1758) from Indian waters

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Abstract

Fishery and population and stock characteristics of *Katsuwonus pelamis* from the seas of the Indian mainland were studied from 2012 to 2017. The average annual landing was 9,843 t, with annual variations from 5,780 to 16,232 t. Major contributions were from the maritime states of Tamil Nadu (3,671 t), Andhra Pradesh (3,173 t) and Kerala (1,790 t). Gillnetters contributed 71.45% to the landings with a catch rate of 1.72 kg unit⁻¹. von Bertalanffy's growth equation was Lt = 85.0 [$1 - e^{-0.50 (t+0.03618)}$] for the western Bay of Bengal (wBoB) and Lt = 95.5 [$1 - e^{0.54 (t+0.03184)}$] for eastern Arabian Sea (eAS), with natural mortality and fishing mortality being 0.85 and 1.37 and 0.86 and 1.13 for these regions respectively. Recruitment was continuous and unimodal along wBoB and bimodal along eAS. The exploitation rate and maximum sustainable yields were 0.62 and 5,761 t for the former region and 0.57 and 2,406 t for the latter region. With present exploitation and yield close to that maximum permissible, stocks are optimally exploited. The maximum relative yield was obtained at the current level of fishing; hence, no further increase in effort is possible. Stock in the Indian mainland waters.

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Introduction

Skipjack tuna (Katsuwonus pelamis), with annual landings of 3.06 million t, is the third most exploited wild fish species globally (FAO, 2016) and forms around 58% of the tuna landings (ISSF, 2020). The species is short-lived, fast-growing and highly fecund, with distribution in the upper mixed layer throughout all tropical and subtropical ocean waters (Kim et al., 2020). The pelagic-oceanic and oceanodromous species aggregates in association with similar-sized tunas of related species (juveniles of yellowfin tuna and bigeye tuna). From the Indian Ocean, the maximum fork length and weight reported for K. pelamis is 80 cm and 10 kg (Grande et al., 2010). Recent tagging and tag recovery studies by the Indian Ocean Tuna Commission (IOTC) indicate a trans-national or trans-oceanic migration pattern. For assessment purposes, the species is considered a single stock (Eveson *et al.,* 2012; Fonteneau and Hallier, 2015) due to large and rapid movements around the Indian Ocean.

Commercial exploitation of oceanic tunas from the Indian waters by fishermen commenced in the late nineties. However, organised fishing is presently being practised in a few isolated regions. The species with a harvestable potential of 0.9 lakh t in the oceanic waters within the Indian EEZ (ISSF, 2020) are caught by purse seines, gill nets, long lines, pole and lines and hand lines. Due to its life-history traits, the species is supposed to support a high harvest rate, nevertheless, with increased catches, concerns have been raised on sustainability. To devise a comprehensive management regime for sustainable exploitation, fishery-related parameters must be studied from the entire migratory trajectory. Reliable stock assessment necessitates information on the temporal distribution of length frequency, age, growth and mortality (Chen and Paloheimo, 1994). As spatiotemporal variability in *K. pelamis* impacts the reproductive dynamics (Schaefer and Fuller 2018), a thorough understanding of region-specific demographics is necessary for strategising management actions leading to judicious resource exploitation. Formulating strategies for optimal utilisation is possible only with effective knowledge of the population and stock characteristics of the species (Sparre and Venema, 1998).

Even though the landings of *K. pelamis* from the Indian EEZ have fluctuated greatly over the last decade, no comprehensive studies on the stock status of the resource are available on a national scale. Studies conducted to date, except for the one by Koya *et al.* (2012), are primarily region-specific; carried out for Andaman waters (Pradeep *et al.*, 2017), Lakshadweep waters (Madan Mohan and Kunhikoya, 1985; Muhsin *et al.*, 2020) and Tuticorin (Ramesh *et al.*, 2019). Therefore, the present study aimed to unravel the population dynamics and elucidate the status of stocks for *K. pelamis* fished along the Indian EEZ. With no pan-India studies available over the last decade, knowledge gained would be used for evolving sustainable management measures for exploiting and managing the species in Indian waters.

Materials and methods

Considering the migratory nature of the resource, coupled with the necessity of area-specific management for offshore resources, the present study classified the Indian marine waters into two distinct zones/regions, *viz*, eastern Arabian Sea (eAS) and western Bay of Bengal (wBoB). Data on annual gear-wise landings and effort from each maritime state during 2012-2017 for *K. pelamis* was obtained from the Fishery Resource Assessment Division of the ICAR-Central Marine Fisheries Research Institute, Kochi. For the eAS region, catch and effort data were pooled for the states of Gujarat, Maharashtra, Daman and Diu, Karnataka and Kerala and for the wBoB region, the same was performed for the states of Tamil Nadu, Andhra Pradesh, Puducherry and Odisha. No landings were reported from Goa and West Bengal during the period.

Random samples of *K. pelamis* were collected weekly from the landing centres in and around Kochi and Vizhinjam for the eAS region and Visakhapatnam and Chennai for the wBoB region. Fork length (FL) for all individuals was measured to the nearest millimetre. Length (FL) frequency obtained in each sampling day was grouped into 2.0 cm class intervals and raised for the day based on the sample weight and the total catch observed for the species on the sampling day. Daily raised length frequencies were summed up for the total observed days in the month and multiplied by the monthly raising factor, considering the total fishing days in that month to arrive at monthly raised numbers (Sekharan, 1962).

Monthly raised length frequencies were analysed using the ELEFAN I module of FiSAT software (Gayanilo et al., 1996) for estimating the von Bertalanffy growth parameters viz, asymptotic length (L₂) and growth coefficient (K). The output of the growth curve was obtained, and the length-based growth performance index (Ø) was calculated from the final estimates of L_{m} and K (Pauly and Munro, 1984). The length at first capture (Lc) was estimated as in Pauly (1984) and the age at zero length (t_0) from Pauly's (1979) empirical equation, Log (-t0) = -0.3922 -0.2752 LogL - 1.038 K. The growth and age were estimated using the von Bertalanffy growth equation, $Lt = L_{m} (1 - e^{-k(t-to)})$. Optimal fishing length (Lopt), the length at which the unfished cohort provides the maximum biomass, was estimated using the equation proposed by Froese and Binohlan (2000). The mid-point of the smallest length group in the catch was taken as length at recruitment (Lr). The recruitment pattern was studied using final estimated values of L_w, K and t_o from the recruitment curve. Lifespan (t_{max}) was estimated at $3/K + t_0$ (Pauly, 1983a). Natural mortality (M) was calculated as in Pauly (1980) by taking the mean sea surface temperature as 28°C and total mortality (Z) from length converted catch curve (Pauly, 1983b) using FiSAT software. Fishing mortality (F) was estimated by F = Z - M. Length structured Virtual Population Analysis (VPA) of FiSAT was used to obtain fishing mortalities per length class. Exploitation rate (E) was estimated from the equation E = F/Z and exploitation ratio (U) from U = F/Z (1 - e^{-z}).

Total biomass and spawning biomass were obtained using the algorithm of Srinath (1998). Maximum sustainable yield (MSY) was estimated following Gulland (1979) for exploited fish stocks as MSY = Z*0.5*B. Relative yield per recruit (Y/R) and biomass per recruit (B/R) at different levels of F were ascertained from the Beverton and Holt Yield per Recruit model using an Excel worksheet.

Results

Fishery

Annual average landings of *K. pelamis* from the Indian waters during 2012-2017 was 9,843 t. Landing increased from 5,780 in 2012 to 7,078 t in 2013 and 11,105 t in 2014. In 2015, catches decreased to 8,302 t; after that in 2016, it increased to 16,232 t and in 2017, landing was 10,559 t. The annual landing for each maritime state is presented in Table 1. Average landings were highest for Tamil Nadu (3,671 t), followed by Andhra Pradesh (3,173 t) and Kerala (1,790 t).

The bulk of the landings were from gillnetters (71.45%), with minor contributions from hooks and lines (9.57%), purse seiners (5.00%) and trawlers (3.40%). The annual average catch rate in gillnets and hooks and lines was 1.72 kg unit¹ and 1.53 kg unit¹ respectively. Percentage contribution by various gears in individual years and annual catch rates in gillnets and hooks and lines are depicted in Tables 2 and 3.

Table 1. Annual skipjack landings (t) in the maritime states along the Indian EEZ during 2012-2017

Years	Odisha	Andhra Pradesh	Puducherry	Tamil Nadu	Kerala	Karnataka	Maharashtra	Gujarat	Daman & Diu
2012	158.7	2984.1	285.4	971.7	274.1	58.4	18.3	650.7	378.8
2013	-	2526.9	328.1	2270.5	814.4	2.8		462.6	672.7
2014	-	7003.8	424.7	2063.6	1201.8	4.2	19.0	328.0	78.5
2015	-	4373.8	121.3	1755.9	853.7	22.1		614.5	560.8
2016	0.9	1484.5	112.0	10111.7	3757.2	24.9	2.9	469.8	268.4
2017	76.1	661.9	99.5	4850.6	3837.8	52.3	0.2	412.9	568.2

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Table 2. Contribution	(%) b	y various gears to	o the landings of K.	pelamis during 2012-2017
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Years	Region	TrawInet	Gillnet	Hook & Line	Ringseine	Non-mechanised	Others
2012	India	11.6	72.2	5.3	4.4	1.3	5.1
	eAS	0.8	79.0	0.6	0.0	2.6	16.9
	wBoB	15.04	70.1	6.8	5.8	0.9	1.3
2013	India	2.5	79.2	3.5	3.0	0.8	10.9
	eAS	1.4	58.7	0.3	0.0	0.0	39.6
	wBoB	2.92	87.1	4.7	4.2	1.2	0.0
2014	India	1.4	68.9	13.1	7.0	0.2	9.3
	eAS	3.7	29.7	2.2	0.0	0.0	64.3
	wBoB	1.04	75.6	14.9	8.2	0.2	0.0
2015	India	0.8	68.8	16.1	4.9	0.4	8.9
	eAS	2.4	58.9	2.6	0.0	0.0	36.2
	wBoB	0.34	72.0	20.6	6.5	0.6	0.0
2016	India	2.5	72.1	7.0	3.1	0.2	15.1
	eAS	1.1	38.9	6.8	0.0	0.0	53.2
	wBoB	3.10	84.9	7.1	4.4	0.3	0.4
2017	India	1.5	67.4	12.5	7.5	0.9	10.2
	eAS	0.5	66.5	9.7	1.7	0.0	21.6
	wBoB	2.28	68.2	14.9	12.5	1.6	0.5

Table 3. Catch rate (kg unit⁻¹) of K. pelamis in gillnets and hooks and lines during 2012-2017

Voor	In	idia	e	AS	W	/BoB	
real	Gillnet	Hook & Line	Gillnet	Hook & Line	Gillnet	Hook & Line	
2012	0.92	0.39	0.68	0.04	1.05	0.53	
2013	1.38	0.37	0.84	0.05	1.66	0.45	
2014	1.81	2.13	0.34	0.23	2.54	2.70	
2015	1.32	2.12	0.74	0.35	1.67	2.66	
2016	3.29	2.44	1.36	2.43	4.39	2.45	
2017	1.97	2.33	2.57	3.97	1.65	1.90	

Around 72% of the landings (annual average of 7,111 t) were contributed from wBoB. More than three-fourths (76.3%) of the catches were from gillnets; with hooks and lines, ring seines and trawl nets contributing 11.5, 6.9 and 4.1%, respectively. Annual average catch rates in gillnets and hooks and lines were 2.09 and 1.70 kg unit⁻¹. Catches from eAS formed 18% (annual average of 2,732 t) of the landings. Gillnets accounted for 55.3% of the catches, with an annual average catch rate of 1.04 kg unit⁻¹.

Population and stock

Population parameters and stock estimates for *K. pelamis* from wBoB and eAS are illustrated in Table 4. The growth and length converted catch curve used in each region for growth and mortality estimation are demonstrated in Figs. 1 (a and b) and 2 (a and b). Size at age and size-wise fishing mortality is portrayed in Figs. 3 and 4. Yield and biomass, Y/R and B/R for fishing effort multiples are presented in Table 5.

wBoB

The primary mode in length composition was at 53.0 cm mid-length (Fig. 5). The fishery was dominated by 1+ year class (34.38 - 54.29 cm) with around 66.8% contribution by number to the landings, followed by 2+ year class (54.30 - 66.37 cm) with a contribution of 26.8%. VBGE was Lt = $85.0 [1 - e^{-0.50} (t + 0.03618)]$. The recruitment pattern was unimodal

and was round the year, with the peak during March-June producing 63.44% of the recruits. Up to 43.0 cm mid-length, natural causes contributed majorly to the loss in the stock thereafter, fishing mortality increased and at 51.0 cm, mid-length eventually overtook natural mortality. Maximum fishing mortality of 2.85 was at 71.0 cm mid-length. Present exploitation (0.62) marginally exceeds the estimated E_{max} of 0.59 and MSY is lower than the average annual catches providing a sense of over-exploitation. However, at the present fishing level, relative yield is highest with maximum yield (7,111 t) and yield per recruit (1,106.7 g); thus, the species is currently optimally exploited in the region.

eAS

The modal length was 59.0 cm mid-length (Fig. 5). Contributions by 0+ (\leq 40.80 cm), 1+ (40.81 - 63.62 cm) and 2+ (63.63 - 76.93 cm) year age groups to the fishery by numbers were 3, 64.5 and 28.7%, indicating a preponderance of 1+ year old class. VBGE was Lt = 95.5 [1 - e^{-0.54} (t + 0.03184)]. Recruitment was substantial throughout the year with two peaks, the major from June-November producing 68.01% of the recruits and the minor from March-April producing 20.63% of the recruits. Mortality was mostly due to natural causes up to 45.0 cm mid-length; henceforth, fishing mortality increased and equalled natural mortality at 65.0 cm mid-length and exceeded thereafter. Fishing mortality was maximum (2.38) at 87.0 cm mid-length. E_{max} estimated was 0.54, slightly lower than the present exploitation (0.57). MSY was close to the annual average yield; thus, the stock appears optimally exploited. Though the



Fig. 1. Monthly length frequency of K. pelamis from (a) wBOB and (b) eAS





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Table 4. Population parameters and stock estimates of *K. pelamis* from Indian EEZ

Parameter	wBoB	eAS
Asymptotic length (L_{∞}) (cm)	85.0	95.5
Asymptotic weight (W_{∞}) (g)	18,650	27,841
Growth coefficient (K) (yr ⁻¹)	0.50	0.54
Growth performance index (ϕ)	3.56	3.69
Length at first capture (L_c) (cm)	31.90	30.55
Age at first capture (t_c) (years)	0.90	0.68
Age at zero length (t_0) (years)	-0.03618	-0.03184
Length at recruitment (L_r) (cm)	21.0	23.0
Age at recruitment (t_r) (years)	0.53	0.48
Lifespan (t _{max}) (years)	5.96	5.52
Optimal fishing length (L _{opt}) (cm)	54.5	61.5
Optimal fishing age (t_{opt}) (years)	2.01	1.88
Natural mortality (M) (yr1)	0.85	0.86
Fishing mortality (F) (yr-1)	1.37	1.13
Total mortality (Z) (yr ⁻¹)	2.22	1.99
Exploitation rate (E)	0.62	0.57
Exploitation ratio (U)	0.55	0.49
Maximum sustainable yield (t)	5,761	2,406
Standing stock biomass (t)	12,927	5,573
Spawning biomass (t)	8,747	4,508
Annual recruitment (millions)	6425.458	1698.324



Fig. 5. Length composition of K. pelamis from wBOB and eAS

1059.4

1040.9

1023.3

1006.8

991.4

977.3

964.3

952.4

1.6

1.8

2.2

2.4

2.6

2.8

3.0

2

marginal increase in relative yield of 0.19% is possible by decreasing the current fishing effort by 20%, with yield and yield per recruit of 2,737 t and 1611.7 g; however, bearing the fact that increment is minimal, it is suggested to continue with the same fishing intensity.

Discussion

The landings of K. pelamis from the waters of the Indian mainland have declined marginally over the last decade, albeit with wide fluctuations. Average landings during 2006-2010 were 14,291 t (Koya et al., 2012), which decreased to 9,843 t during 2012-2017. During the seventies and eighties, several hundred to a few thousand tonnes were being landed, which steadily increased due to horizontal expansion in fishing operations to deeper oceanic waters and as a result, in 2007, historic highs in landings to the tune of 27,127 t (including both mainland and island) were recorded (Koya et al., 2012). Catches have fallen henceforth; however, recent years have shown signs of recovery in the fishery. The contribution of gillnets has increased over the decade at the expense of other gears, particularly hooks and lines. Region-wise landing patterns, however, have remained the same, with the maritime states of Tamil Nadu, Andhra Pradesh and Kerala contributing majorly to the mainland landings. Due to the narrow continental shelf and steep slope, fishermen in these states can reach the offshore oceanic waters readily and thus, catch this accessible resource efficiently. Catch rates in gillnets and hooks, and lines were similarly higher along the wBoB compared to eAS for the topographical reasons mentioned above.

Using population parameter information, fish stock assessment forms the basis for efficient resource management and for predicting the responses of stocks to these management measures. In the absence of direct age determination from hard parts (markings on scales and vertebrae), the present study used length frequency for arriving at age and growth. The sample size of the population was 16,023 for eAS and 3,365 for wBoB, much higher than required (1,500) for arriving at reliable estimates of age and growth (Pauly, 1987). Growth and mortality parameters reported from various parts of the Indian Ocean are shown in Table 6. The asymptotic length was lower in wBoB, primarily due to

3105.4

2712.3

2399.7

2146.3

1937.5

1763.0

1615.3

1489.0

1415.8

1225.5

1074.4

952.2

852.0

768.6

698.4

638.7

E (v) multiplier	Y/R (g)		Y (t)		B/R	(g)	B (t))
r (x) multiplier	wBoB	eAS	wBoB	eAS	wBoB	eAS	wBoB	eAS
0	0	0	0	0	0	0	0	0
0.2	721.6	1005.5	4636.8	1707.7	2633.7	4449.1	16922.6	7556.1
0.4	982.1	1408.3	6311	2391.8	1792.2	3115.8	11516	5291.6
0.6	1077.4	1564.6	6923.2	2657.2	1310.8	2307.6	8422.3	3919.1
0.8	1106.3	1611.7	7108.5	2737.2	1009.4	1782.9	6485.8	3027.9
1	1106.7	1608.6	7111	2732.0	807.8	1423.6	5191	2417.7
1.2	1094.8	1582.6	7034.5	2687.7	665.9	1167.1	4278.9	1982.1
1.4	1077.9	1546.6	6925.8	2626.6	562.0	977.6	3611.0	1660.3

483.3

422.1

373 5

334.0

301.5

274.4

251.4

231.7

833.6

721.6

632.6

560.7

501.6

452.6

411.2

376.1

2559.7

2492.6

2428.0

2367.2

2310.5

2258.1

2209.7

2165.2

Table 5. Yield (Y), Biomass (B), Yield per recruit (Y/R) and Biomass per recruit (B/R) for different multiples of fishing effort (F) for K. pelamis from eastern Arabian Sea (eAS) and western Bay of Bengal (wBoB)

6807.0

6688.5

65751

6468.9

6370.5

6279.8

6196.4

6119.8

1507.2

1467.7

14297

1393.8

1360.5

1329.6

1301.1

1274.9

Study area	L _m (cm)	K (yr ⁻¹)	t _o (years)	M (yr¹)	F (yr-1)	Z (yr-1)	Authors
Indian Ocean	60.6	0.93					Marcile and Stequert (1976)
Lakshadweep	84.2	0.22	-				Appukuttan <i>et al</i> . (1977)
Lakshadweep	90.0	0.49	-0.06				Madanmohan and Kunhikoya (1985)
Sri Lankan waters	77.0	0.52					Sivasubramanium (1985)
Indian seas	66.0	1.1	-				Yohannan <i>et al.</i> (1993)
Lakshadweep	92.6	0.98	-0.01	1.04	6.93	7.97	Sivadas et al. (2003)
Lakshadweep	76.65	0.95		1.33	2.39	3.72	Sivadas et al. (2005)
Chennai				1.92	2.78	4.70	Kasim and Mohan (2009)
Indian seas	92.0	0.50	-0.0012	0.55	0.85	1.41	Saidkoya <i>et al.</i> (2012)
Andaman	74.6	0.59	-0.21	0.93	1.14	2.07	Pradeep <i>et al.</i> (2017)
Tuticorin	95.7	0.40		0.73	0.90	1.63	Ramesh <i>et al.</i> (2019)
Lakshadweep	72.5	0.48	-0.1097	0.82	1.51	2.33	Muhsin <i>et al</i> . (2020)
Oman Sea	88.0	0.3	-0.41	0.58	0.3	0.88	Hashemi <i>et al.</i> (2021)
Indonesian waters	60.75	0.28	-0.309	0.64	0.97	1.61	Kantun <i>et al.</i> (2021)

Table 6. Growth and mortality estimate for *K. pelamis* in the Indian Ocean

the lower length ranges of sampled fishes. Differences in gillnet mesh sizes operated in both regions might have contributed to the variations observed in the length classes. Stequart and Marsac (1989) have noted skipjack tuna in the Indian Ocean to range between 20-80 cm in size, with differences attributed to the fishing techniques used. Modal lengths are in accordance with earlier reports (Yohanan et al., 1993; Sivadas et al., 2003). The growth coefficient reported (0.50 - 0.54) represents a moderate growth rate for the species. Slight higher growth coefficient along eAS is suggestive of higher growth rates. Trophic enrichment caused by monsoon upwelling provided favourable biological situations, resulting in higher growth along the eAS. The growth performance index is consistent for a particular species; exerting a compensatory control on L_a and K estimates (Sparre and Venema, 1998). Results obtained presently are consistent with recent reports for the species (Muhsin et al., 2020; Hashemi et al., 2021). Growth differences between individuals, populations and cohorts are often substantial and usually genetic, but also dependent on physical, biotic and environmental conditions (Sparre and Venema, 1998); the same appeared true globally for the present species. The 1+ year age group dominated the fishery. During the 1st year of life, the highest growth increment in length was recorded, after that, it decreased with increasing age. The species is reported to live between four and six years (Pradeep et al., 2017; Muhsin et al., 2020; Hashemi et al., 2021), in tune with our findings. Sexual maturity size for the species in the Indian waters was estimated at 41 cm (Kova et al., 2012), therefore, along both eAS and wBoB, present lengths at first capture are lower than the length at sexual maturity, providing evidence that most of the individuals were caught before they matured and spawned. This indicates that the spawning stock is severely stressed, and increasing gear mesh sizes for increasing their sizes and ages at exploitation is essential for avoiding the catch of juveniles.

Natural mortality and the growth coefficients for a fish are directly related, and natural mortality and the asymptotic length and the life span are inversely related (Beverton and Holt, 1956). A similar phenomenon was observed in *K. pelamis* from both regions.

According to Pauly (1980), the age of the species and the predator abundance in the environment influence the natural mortality coefficient. The M/K ratio explains the relationship between natural mortality and physiological factors. The present ratio was between 1.59 and 1.70,

within the proposed optimum range (Beverton and Holt, 1959). The predominance of growth on mortality is determined by the Z/K ratio (Barry and Jegner, 1989). A ratio close to unity indicates a steady-state population and a ratio over 2 indicates overexploited stocks and a mortality-dominated population. The observed pattern of size-wise fishing mortality with intense pressure on the middle to upper length classes is a typical feature of the gillnet fishery. The exploitation rate of 0.61 and 0.58 also indicates that exploitation is marginally higher than optimum.

The existence of mature individuals indicates round-the-year spawning for the species, with a major peak during December-March and a minor peak during June-August (Stequert and Ramcharrun, 1996; Koya *et al.*, 2012). This spawning results in continuous recruitment (Sivadas *et al.*, 2003). In accordance with Pradeep *et al.* (2017), along wBoB, recruitment was unimodal, while along eAS, two spikes in recruitment patterns were observed.

Population parameters, indicative of distinct stocks, are similar for eAS and wBoB. Growth coefficient and growth performance index, lengths at first capture and recruitment, lifespan and natural mortality are comparable for both these regions; thus, it is evident that a unit stock of K. pelamis exists in the mainland waters of India. With higher standing and spawning stock biomass, recruitment was superior along wBoB. For both regions, present exploitation and yield are marginally higher than E_{max} and MSY and the relative yield percentage is either maximum or near maximum for the current fishing effort. Therefore, it is logically concluded that the species in the waters of the Indian EEZ is optimally exploited. Generally, skipjack tuna with high turnover rates are relatively less vulnerable to fishing pressure (Kleiber et al., 1987). Future expansion of the fishery for increasing production should be to the less exploited areas (oceanic islands, shelf break areas, seamounts and knolls/submerged banks, sea ridges and reef areas), known for high resource concentrations.

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