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Decrypting the life history characteristics and stock dynamics of *Parapenaeopsis stylifera* (Milne-Edwards, 1837) in the north-western Bay of Bengal: A confluence of approaches for better decision support

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Abstract

The life history of Kiddi shrimp (*Parapenaeopsis stylifera*) was assessed using length-based data from the commercial trawlers operated along the Digha waters (West Bengal, India). Growth parameters were estimated as L_∞ = 14.26 cm, K = 1.77 yr^{-1}, t_0 = -0.001 yr^{-1}, t_{max} = 1.5 yr and φ = 2.56. Mortality rates were M = 3.00 yr^{-1}, F = 4.11 yr^{-1}, Z = 7.11 yr^{-1}, with an exploitation rate (E) of 0.58. The species matures early (L_{m50} ≈ 8.15 cm, 0.48 yr) and attains peak biomass (L_{opt} ≈ 8.0 cm, 0.47 yr). A high M/K ratio (1.7) indicates r-selected traits-fast growth, high mortality, and peak yield at high fishing mortality. Cohort biomass declines rapidly to 1% within 0.65 yr, yet the short generation time allows reproduction under current exploitation. Stock status from the Bayesian Schaefer Model using catch-based data (2007-2021) showed current biomass (B/B_{msy} = 1.15) is 15% higher, whereas the effort (F/F_{msy} = 0.85) is 15% lower than required level for MSY. Kobe plot also indicates a higher probability (57.9%) that the stock is in the healthy and sustainable green zone. Thompson and Bell analysis suggested fishing mortality could increase by 8%, raising yield marginally by 1.6% to 2442 t and revenue by 1.3% to ₹423 million, while maintaining safe spawning biomass (SSB/SSB_0 =30%). However, due to its short generation time and recruitment sensitivity, *P. stylifera* requires adaptive harvest control rules with annual or biannual assessments to ensure long-term sustainability.

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Introduction

West Bengal, with a 158 km coastline and a 17,049 km² continental shelf, is part of the Bay of Bengal Large Marine Ecosystem (BBLME). Nourished by the Ganges-Brahmaputra riverine systems, it hosts the Sundarbans mangroves and the Hooghly-Matla Estuary, which provide ideal breeding and nursery grounds for important fisheries in the region (Dutta *et al*., 2016; Datta *et al*., 2022). About 3.7 lakh fisherfolk depend on this sector, which contributes roughly 2 lakh t (around 7% of India's total marine fish landings). The catch mainly comprises pelagic (52%), demersal (32%), and crustacean (14%) resources (CMFRI-FSI-DoF, 2020; CMFRI, 2022). Among the crustaceans, *Parapenaeopsis stylifera* (Milne-Edwards, 1837), commonly known as kiddi shrimp, accounts for about 1% of the state's total marine fish landings. However, it is regarded as a commercially important species because it contributes nearly 10% of the annual crustacean catch in West Bengal.

P. stylifera belongs to the family Penaeidae and is widely distributed across the Indian Ocean from Kuwait to Indonesia. Unlike other penaeid shrimps, the species is a purely marine species, as it completes all of its early life developmental stages in marine environment (Rao, 1965). This is a benthic-dwelling species that prefers soft substrata ranging from muddy to sandy bottoms and is usually found at a depth of 50 m (Holthuis, 1980; Carpenter *et al*., 1997). Considering the fisheries significance of *P. stylifera*, several studies have been made to understand its larval development in Kerala waters (Muthu *et al*., 1978); growth performance in Mangalore (Anantha *et al*., 1997), Calicut (Sarada, 2002) and Saurashtra (Dineshbabu, 2005) coasts; population dynamics in Kerala (Suseelan *et al*., 1998; Sarada, 2002); reproductive biology in Kerala (Geetha and Nair, 1992) as well as feeding behaviour in Visakhapatnam (Sudha *et al*., 2013) coasts of India. There are few studies from abroad where observations have been made to understand the population dynamics of *P. stylifera* in Kuwait (Mathew *et al*., 1987; Mohammed *et al*., 1998), Iran (Safaie, 2017), Indonesia (Suradi *et al*., 2017) and Pakistan (Mohsin *et al*., 2017) coasts.

Nevertheless, despite its commercial importance along the north-east coast of India, there is still no scientific information about the life history characteristics, population dynamics and status of the species in the region, which necessitates a focused study on this species, especially under the present scenarios where the overall marine landings are fluctuating erratically. Therefore, the present study was envisaged to generate information on the life-history parameters and exploitation status of *P. stylifera* in West Bengal waters which was used both in the data-poor Bayesian Schaefer model (Froese *et al*., 2017) and the data-moderate dynamic pool analytical model (Thompson and Bell, 1934) to derive a decision support framework so that appropriate management strategies can be developed for ensuring the sustainable utilisation of the resource.

Materials and methods

Temporal size composition, fishing effort and landings data were collected at fortnightly intervals for a period of about 3 years from July 2018 to March 2021 from the commercial trawlers operated along the Digha coast in West Bengal, India. The total body length (TL) of 3853 specimens was measured as the straight-line distance from the tip of the rostrum to the tip of the telson using a digital vernier caliper (Insize 1126-300). Body weight of the specimens was also recorded with an electronic balance (Aczet CY225C). The data collected at fortnightly intervals were raised to the monthly estimates of West Bengal by multiplying with the raising factors (RFs) derived using landings data obtained from the National Marine Fishery Resources Data Centre (NMFDC) of the ICAR-Central Marine Fisheries Research Institute (ICAR-CMFRI), Kochi, India using the following formula:

$$RF = \frac{\text{Total monthly species landings of the state}}{\text{Total monthly sample weight of the species}}$$

Growth parameters

The growth of the shrimp was modeled using growth function (VBGF) suggested by von Bertalanffy (1938) as given below and the model parameters were estimated using the TropFishR package by performing electronic length frequency analysis with a genetic algorithm (ELEFAN_GA) routine (Mildenberger *et al*., 2017; Schwamborn *et al*., 2019). The jackknife technique (Tukey, 1986) was used to estimate the 95% bootstrap percentile confidence intervals around the mean VBGF growth parameters.

$$L_t = (L_\infty \times (1 - \exp^{-k(t-t0)}))$$

where, L_∞ is the asymptotic length in cm; K is the growth co-efficient in yr^{-1}; t_0 is the age of the individual when the length was theoretically zero; L_t is the length at time t and t is the time at which the length is projected.

The growth performance index (φ') was calculated using the following formula recommended by Pauly and Monro (1984):

$$\varphi' = Log_{10}(K) + 2Log_{10}(L_\infty)$$

where, L_∞ is the asymptotic length in cm; K is the VBGF growth coefficient in yr^{-1}

The age at zero length (t_0) was back calculated using the rearranged VBGF equation (von Bertalanffy, 1938):

$$t_0 = \frac{1}{K} \ln\left[1 - \left(\frac{L_0}{L_\infty}\right)\right]$$

where, L_∞ is the asymptotic length in cm; K is the VBGF growth coefficient in yr^{-1} and L_0 is the length at birth, which has been fixed at 0.027 cm based on the size of the nauplius-1 following Muthu *et al*. (1978).

In the absence of direct observation data on the age of the largest individual, the t_{max} was indirectly estimated following the conceptual framework recommended by Pauly (1983) using the generalised equation as mentioned below:

$$t_{max} = \frac{-\ln\left(1 - \frac{L_{max}}{L_\infty}\right)}{K} + t_0$$

where, L_{max} and L_∞ are the maximum observed length and the asymptotic length in cm for the species; K is the VBGF growth coefficient in yr^{-1} and t_0 is the age of the individual when the length was theoretically zero.

Length-weight relationship (LWR)

The relationship between total length and body weight for the species (n = 1200) was established using the power law (Le Cren, 1951) following the appropriate modeling framework suggested by Dash *et al*. (2023). Wald test was performed to check if the growth is isometric (b = 3.0) or allometric (b ≠ 3.0).

$$W = a(TL)^b$$

where, W is the body weight in 'g'; TL is the total length in 'cm'; a and b are model parameters.

Mortality and exploitation parameters

The natural mortality (M) was estimated following Quinn and Deriso (1999) using the following generalised formula:

$$M = \frac{-\ln(p)}{t_{max}}$$

where, p is the proportion of animals that survive by the time they reach maximum age *i.e.*, t_{max} and M is the natural mortality in yr^{-1}.

The instantaneous total mortality rate (Z) was estimated by applying the length-converted linearised catch curve method (Pauly, 1983) using the 'catchCurve' routine in the 'TropFishR' package. The annual fishing mortality rate (F) was determined by subtracting M from Z (*i.e.*, F= Z-M), and the current exploitation rate (E_{cur}) was computed using the formula E=F/Z (Ricker, 1975).

Length at capture (L_{c50})

The mid-length of the smallest length-class caught during the study period was taken as length at recruitment (L_r). The length at which 50% of the shrimps in a population becomes vulnerable to the fishing gear (*i.e.*, L_{c50}) was estimated by performing a logistic regression with the probability of capture of sequential length classes calculated from the backward extrapolation of the regression line of the descending limb of the length-converted catch curve (Pauly, 1984). The following formula was used for the logistic regression:

$$p_{TL} = \frac{\exp^{[a+b(TL)]}}{1 + \exp^{[a+b(TL)]}}$$

where p_{TL} is the extrapolated probability of capture at length TL, a and b are the estimated coefficients of the logistic equation, and TL is the total length of the shrimp in cm. L_{c50} was estimated as the negative ratio of the coefficients (-a/b). The analysis was performed using the 'catchCurve' routine with 'calc_ogive' logic set to TRUE in the 'TropFishR' package.

Length at maturity (L_{m50})

The length at which 50% of the shrimps in a population becomes mature (*i.e.*, L_{m50}) was estimated by performing a logistic regression with the probability of maturity of sequential length classes. The shrimps (n = 1029) were categorised into 5 different stages of maturity depending on the size and appearance of the ovary following King (1995). The shrimps that have completed stage-3 and spent shrimps were considered as matured and the proportion of such matured shrimps in sequential length classes was regressed using the following formula (Ashton, 1972):

$$p_{TL} = \frac{\exp^{[a+b(TL)]}}{1 + \exp^{[a+b(TL)]}}$$

where p_{TL} is the predicted maturity proportion at length TL, a and b are the estimated coefficients of the logistic equation and TL is the total length of the shrimp in cm. L_{m50} was estimated as the negative ratio of the coefficients (-a/b). The analysis was performed using the generalised linear model 'glm' routine with binomial distribution and 'link' set to 'logit'.

Length-based cohort analysis (Lcohor)

Estimation of the stock biomass, yield and recruitment, as well as fishing mortalities for each length-class was made by performing a length-based cohort analysis (Lcohor) following Jones (1984). In Lcohor, the number of survivours in a length-class (N_1) was calculated in a reverse order from its immediate next higher length-class (N_2) starting from the number of survivours in the terminal length-class ($N_t = C_t/E_t$, where, C_t and E_t are the catch number and assumed terminal exploitation rate of 0.5 in the last or highest length-class, respectively) using the following formula:

$$N_1 = [N_2 \times M\ factor_1 + C_1] \times M\ factor_1$$

where $M\ factor_1$ is the natural mortality factor of the preceding length-class (L_1) calculated from the immediate next length-class (L_2) using the following equation:

$$M\ factor_1 = \left[\frac{L_\infty - L_1}{L_\infty - L_2}\right]^{\frac{M}{2k}}$$

The fishing mortality rate (F) of each length-class was calculated from the natural mortality (M) and the corresponding exploitation rate (E) using the equation mentioned below:

$$F_1 = M \times \frac{E_1}{1 - E_1} \text{ where, } E_1 = \frac{C_1}{N_1 - N_2}$$

where, the exploitation rate (E_1) of a length-class (L_1) was calculated from the catch number (C_1) and the total number of fish that would be lost (N_1-N_2) between L_1 to L_2.

The mean number of survivors (N_1) in a length-class (L_1) was calculated by dividing the total loss (N_1-N_2) in the length-class with the total mortality (Z) and the corresponding mean biomass (B_1) was obtained by converting the mid-length of the length-class to the mean-weight of the length-class using the LWR ($a \times L_1^b$) and then multiplying with the mean number of survivours in the length-class as follows:

$$\overline{B}_1 = \overline{N}_1 \times a \times L_1^b \text{ where, } \overline{N}_1 = \frac{N_1 - N_2}{Z_1}$$

The individuals in the length classes on and above the length at maturity (L_{m50}) were considered mature and their biomass was used as spawning stock biomass (SSB).

The mean yield (Y_1) from the length-class (L_1) was obtained by converting the mid-length of the length-class to the mean weight of the length-class using the LWR ($a \times L_1^b$) and then multiplying it with the mean number of individuals caught in the length-class as follows:

$$\overline{Y}_1 = \overline{C}_1 \times a \times L_1^b \text{ where, } \overline{C}_1 = \text{is the mean catch number of } L_1$$

The analysis was performed using the virtual population analysis (VPA) routine with 'analysis_type' set to cohort analysis (CA) in TropFishR package.

L_{opt}, *i.e.*, the mid-length of the length-class at which the mean biomass of the cohort attains its maximum (B_{max}) was directly estimated from the above-mentioned cohort analysis and compared with the below-mentioned empirical estimate of L_{opt} derived from L_∞ suggested by Holt (1958) and Beverton (1992):

L_{opt} = Length corresponding to B_{max} of Lcohor compared with the

$$L_{opt} = \frac{b}{b + \frac{M}{K}} = L_\infty \frac{3}{3 + \frac{M}{K}}$$

where, L_∞ is the asymptotic length in cm; K is the growth co-efficient in yr^{-1}; M is the natural mortality in yr^{-1} and b is the power coefficient in the LWR, which has been assumed to be 3.

Similarly, L_{c_opt}, *i.e.,* the length of capture at which the mean length in the catch becomes equal to the cohort's L_{opt}, as a result of which the biomass of the catch becomes maximum for a given fishing pressure, was estimated directly from Lcohor-derived L_{opt}, *i.e.,* L_{opt_Lcohor} (instead of L_∞ derived L_{opt}) following the empirical equation suggested by Froese *et al*. (2016c) as follows and was compared with the current L_{c50} derived from the length converted catch curve method.

$$L_{copt\_lcohor} = L_{copt\_lcohor}\left(\frac{\frac{2}{3}+\frac{F}{M}}{b+\frac{F}{M}}\right) \text{ instead of } L_{copt} = L_\infty \frac{\left(2+3\frac{F}{M}\right)}{\left(1+\frac{F}{M}\right)\left(3+\frac{M}{K}\right)}$$

where, L_{opt_Lcohor} is the length from Lcohor analysis at which the mean biomass of the cohort attains its maximum; L_∞ is the asymptotic length in cm; K is the growth co-efficient in yr^{-1}, M and F are the natural and fishing mortality in yr^{-1} and b is the power coefficient in the LWR, which has been assumed to be 3.

Stock assessment

Long-term stock status

A Bayesian state-space implementation (BSM) of the Schaefer model (Schaefer, 1954) was applied following the approach suggested by Froese *et al*. (2017) using the CMSY++ R package to get an initial estimate on the fisheries reference points (MSY, F_{msy} and B_{msy}), the relative stock size (B/B_{msy}) and exploitation (F/F_{msy}), using the long-term catch and abundance time-series data (CPUH, *i.e.,* catch per unit hour), species resilience (high resilience with user defined r range from 1 to 1.5) and qualitative stock status knowledge of *P. stylifera* during the period 2007 to 2021. In BSM, a feature of the Monte Carlo method was used to select the most viable biomass trajectory for the subsequent years generated using a modified Schaefer surplus production model according to the equation mentioned below:

$$B_{t+1} = B_t + \left(4\ \frac{B_t}{k}\right) r \left(1 - \frac{B_t}{k}\right) B_t - C_t$$

where, B_{t+1} is the biomass in the next year, B_t is the present biomass and C_t is the present year catch, r is the intrinsic population rate and k is the carrying capacity. The modified Schaefer surplus production model uses an extra multiplier of 4 B_t/k (which is 1 at 0.25 k but becomes zero at zero k), that linearly decreases recruitment towards zero at zero k only when the biomass falls below 0.25 k (*i.e.,* $B_t/k < 0.25$). JAGS program with the Markov chain Monte Carlo process was used to sample the probability distributions of the parameters (Plummer, 2003; Thorson, 2014). The geometric means of the resulting density distributions of r, K and MSY were used to derive the managerial reference points (MSY, F_{msy}, B_{msy}).

Short-term stock status

The estimates on recruitment and the length-class-wise biomass, spawning stock biomass and yield derived by the Lcohor analysis using the short-term length frequency data on *P. stylifera* during the period 2018 to 2021 were further used in a length-based Thompson and Bell model (1934) to simulate the effect of different levels of fishing pressure (F) on the annual yield (Y), revenue (R), total biomass (B) and spawning stock biomass (SSB) using the 'predict_mod' routine with model type set to 'ThompBell' in the TropFishR package. To simulate the effect of certain changes in fishing effort (for example, x time change in F), the corresponding Fs of the lengh-classes obtained from Lcohor were multiplied with the 'x' and then added with the M (which was assumed constant throughout the length-classes) to derive the new Zs (total mortality rates), which were used to calculate the number of survivours (N_2) in respective length-classes (L_2) in a straight order from the number of survivours (N_1) in its previous length-class (L_1) starting from the number of recruits (which is the number of survivours in the lowest length-class L_r) obtained from Lcohor using the following formula:

$$N_2 = N_1 \times \frac{\frac{1}{M\ factorL_1} - \frac{F_1}{Z_1}}{M\ factorL_1 - \frac{F_1}{Z_1}}$$

where, M $factor_{L1}$ is the natural mortality factor; F_1 and Z_1 are respectively the new fishing and total mortality rates of the preceding length-class (L_1) derived by multiplying with the intended change in fishing effort (*viz.,* x time change in F).

The new mean catch numbers (C_1) in the corresponding length classes (L_1) were derived from its survivours (N_1) and the survivours (N_2) of the next higher length class (L_2) using the following formula:

$$\overline{C}_1 = (N_1 - N_2) \times \frac{F_1}{Z_1}$$

The new mean yield (Y_1) from the length-class (L_1) was obtained by converting the mid-length of the length-class to the mean-weight of the length-class using the LWR ($a \times L_1^b$) and then multiplying it with the new mean catch number (C_1) of the length-class as follows:

$$\overline{Y}_1 = \overline{C}_1 \times a \times L_1^b \text{ where, } \overline{C}_1 = \text{is the mean catch number of } L_1$$

The mean number of survivours (N_1) in a length-class (L_1) was calculated by dividing the total loss (N_1-N_2) in the length-class with the total mortality rate (Z) as follows and the corresponding mean biomass (B_1) was obtained by converting the mid-length of the length-class to the mean-weight of the length-class using the LWR ($a \times L_1^b$) and then multiplying it with the mean number of survivours of the length-class as follows:

$$\overline{B}_1 = \overline{N}_1 \times a \times L_1^b \text{ where, } \overline{N}_1 = \frac{N_1 - N_2}{Z_1}$$

The individuals in the length classes on and above the length at maturity (L_{m50}) were considered mature and their biomass was used as spawning stock biomass (SSB). The revenue from each length class was obtained by multiplying the unit selling price of the length classes with their respective mean biomass (B_1).

Results and discussion

Fishery

The annual catch and catch rate (CPUH) trends of the species during 2007-2021 along the West Bengal coast are shown in Fig. 1a.

During 2017, the species showed its highest-ever historic landings (about 3917 t). The catch, however, declined by 59% during the next year (2018) due to a 51% reduction in efforts (AFH), after which an increase in the catch trend can be clearly seen (Fig. 1a). In 2021, despite a drastic drop of 34% in standardised effort, the decrease in landings was only about 7%, which can be considered a sign of the increase in abundance. The wide fluctuations in fishing efforts are mainly due to the erratic and frequent incidences of cyclonic storms in the Bay of Bengal, which have reduced the overall number of active fishing days during a season. Furthermore, as the fishery along the coast is highly demand-driven, any shift in demand affects the landings. During the last four years (2018-2021), on average 2488 t of *P. stylifera* were landed every year.

During the same period, the species contributed about 10% to the shrimp landings, 9% to the total crustacean landings and about 1% to the total marine fish landings in West Bengal (Fig. 1b). The species increasingly landed during the monsoon and winter seasons (during the last two quarters of the year) (Fig. 1c). The species is mainly harvested by multiday trawlers (84%), followed by bag netters (3%), gill netters (2%) and other mechanised gears, which together contributed 11% to the species total landings (Fig. 1d).

Life-history parameters

Since it is difficult to implement resource management strategies differently and separately for males and females that share the same geographical and ecological distribution and are subjected to the same exploitation conditions, sex-pooled data has been used in the analysis. The population life-history parameters of *P. stylifera* derived using sex-pooled data are given in Table 1 and have also been compared with the earlier studies in Table 2 and Fig. 2. In the present study, both the median of L_∞ and K were slightly higher compared to the earlier studies (Fig. 2).

As a rule of thumb, the species that confirms Beverton-Holt life history invariants (BH-LHI) shows a L_{max}/L_∞ ratio of 0.95 (Pauly, 1984; Hordyk *et al*., 2015). Though the ratio is more or less the same for closely related species, for the short-lived fast-growing species it tends to be lower than 0.95 (resulting in a $L_\infty > L_{max}/0.95$) but becomes higher than 0.95 for the long-lived slow-growing species, resulting in a $L_\infty < L_{max}/0.95$ (Mathews and Samuel, 1990a). *P. stylifera* being an r-selected species, the lower L_{max}/L_∞ ratio of 0.93 observed in the present study can be considered reasonable. As the estimation of L_∞ is largely influenced by the L_{max}, it is often affected by spatio-temporal factors such as habitat temperature, fishing pressure and gear selectivity and therefore, varies from location to location. However, for any given species, this spatio-temporal variation in L_∞ is usually compensated by the growth coefficient (K) and therefore, the growth performance index (φ') that depends both on L_∞ and K remains more or less similar or range-bound for the species. The φ' has the dimensions of both length and time, is less liable to bias, and is usually normally distributed with a smaller standard deviation compared to other growth indices; therefore, it has been recommended as the most flexible and precise estimator of growth performance (Mathews and Samuel, 1990b). The φ' obtained in the present study is higher compared to the earlier studies, which implies better growth of *P. stylifera* along the north-east coast of India. The higher φ' reported for the species by the earlier studies from abroad, *i.e.*, Kuwait (Mohammed *et al*., 1998), Iran (Safaie, 2017) and Indonesian (Suradi *et al*., 2017) waters are doubtful as the carapace length (mm) has been used in these studies instead of the recommended total length (cm)

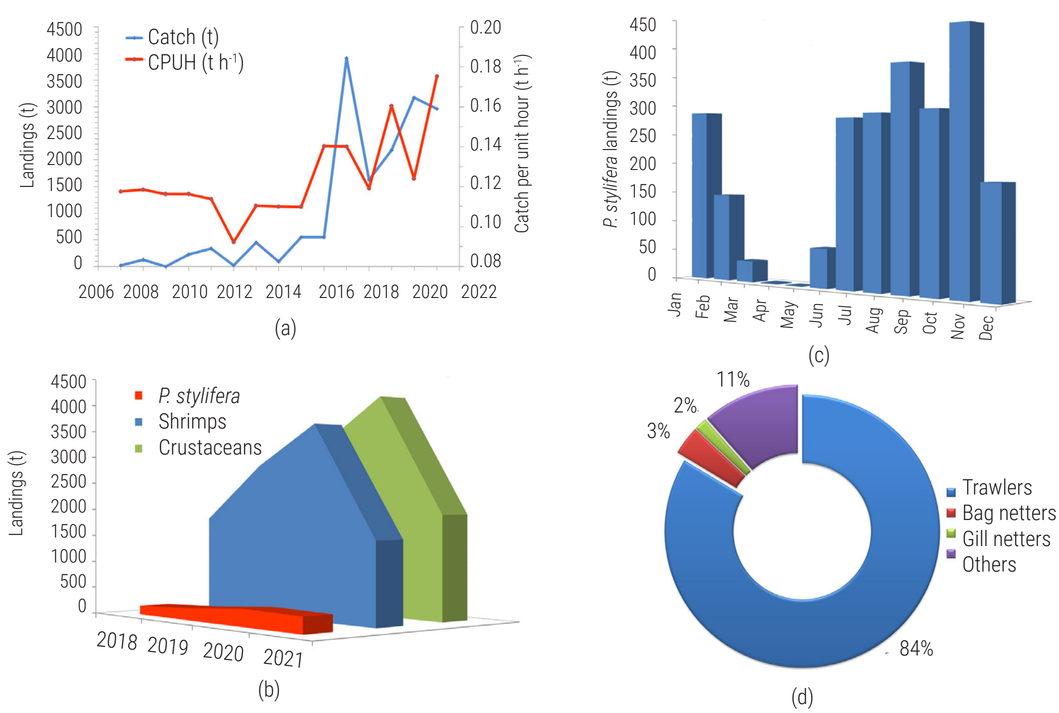

Fig. 1. Fishery profile of *P. stylifera* along the West Bengal coast. (a) Annual catch and catch rate trend during 2007-2021; (b) Monthly average catch trend during 2018-2021; (c) Contribution of *P. stylifera* landings to the total crustacean and shrimp landings of the state and (d) Percentage contribution to the total landings of the species by different gears

Table 1. Population life history and exploitation parameters of *P. stylifera* in West Bengal waters during 2018 and 2021

Parameters	Mean	CI	Parameters	Mean	CI
L_{∞} (cm)	14.26	14.08-14.37	L_{c50} (cm)	8.16	7.89-8.52
K (yr^{-1})	1.77	1.57- 1.89	L_{c75} (cm)	8.50	8.19-8.90
t_o (yr)	-0.0010	-0.0010 – -0.0009	L_{c95} (cm)	9.02	8.67-9.49
Φ'	2.56	2.50- 2.58	t_{c50} (yr)	0.48	0.45-0.51
t_{max} (yr)	1.5	1.59-1.92	t_{c75} (yr)	0.51	0.48-0.55
M (yr^{-1})	3.00	2.50-3.21	t_{c95} (yr)	0.57	0.53-0.62
Z (yr^{-1})	7.11	6.25-7.96	L_{m50} (cm)	8.15	7.92-8.32
F (yr^{-1})	4.11	3.25-4.96	L_{m75} (cm)	8.51	8.34-8.67
E	0.58	0.52-0.62	L_{m95} (cm)	9.10	8.91-9.40
L_{opt_Lcohor} (cm)	8.00	NA	t_{m50} (yr)	0.48	0.46-0.50
$L_{c\_opt\_Lcohor}$ (cm)	6.98	NA	t_{m75} (yr)	0.51	0.50-0.53
Recruits (nos.)	1584964406	NA	t_{m95} (yr)	0.57	0.55-0.61
Resilience, Initial and Current exploitation and stock biomass status (BSM approach)					
Parameters	Mean	CI	Parameters	Mean	CI
r	1.12	0.91-1.36	MSY (1000 t)	3.01	2.17-5.58
k or B_0 (1000 t)	10.80	7.32-21.50	Catch (1000 t)	2.96	NA
B_{cur} (1000 t)	6.17	3.63-11.70	Catch/ MSY	0.99	0.53-1.36
B_{msy} (1000 t)	5.40	3.66-10.80	B_{cur}/k	0.58	0.30-0.77
F_{msy}	0.56	0.45-0.68	B_{cur}/ B_{msy}	1.15	0.61-1.54
F_{cur}	0.47	0.24-0.88	F_{cur}/ F_{msy}	0.85	0.44-1.56
Initial and Current exploitation and stock status (Thompson and Bell approach)					
R_{cur} (Million ₹)	417.68	B_0 (t)	2490.96	SSB_0 (t)	1803.01
Y_{cur} (t)	2403.59	B_{cur} (t)	1082.62	SSB_{cur} (t)	571.80
F_{cur}	4.11	B_{cur} /B_0	0.43	SSB_{cur}/SSB_0	0.32
Management reference points in the context of growth-overfishing (Thompson and Bell approach)					
Considering F_{max} as a target reference point		Considering F_{mey} as a target reference point		Considering $F_{0.1}$ as a target reference point	
F_{max} (yr^{-1})	14.05	F_{mey} (yr^{-1})	9.17	F_{01} (yr^{-1})	3.58
Rel_F_{max} (times)	3.42	Rel_F_{mey} (times)	2.23	Rel_F_{01} (times)	0.87
Y_{max} (t)	2673.02	Y_{mey} (t)	2649.28	Y_{F01} (t)	2326.29
R_{max} (Million ₹)	439.77	R_{mey} (Million ₹)	444.17	R_{F01}(Million ₹)	406.50
B_{max} (t)	662.27	B_{mey} (t)	772.50	B_{F01} (t)	1150.13
SSB_{max} (t)	258.86	SSB_{mey} (t)	334.42	SSB_{F01} (t)	626.59
Y_{cur}/ Y_{max}	0.90	Y_{cur}/ Y_{mey}	0.91	Y_{cur}/ Y_{F01}	1.03
B_{cur}/ B_{max}	1.63	B_{cur}/ B_{mey}	1.40	B_{cur}/ B_{F01}	0.94
B_{max} /B_0	0.27	B_{mey} /B_0	0.31	B_{F01} /B_0	0.46
SSB_{cur}/ SSB_{max}	2.21	SSB_{cur}/ SSB_{mey}	1.71	SSB_{cur}/ SSB_{F01}	0.91
SSB_{max}/SSB_0	0.14	SSB_{mey}/SSB_0	0.19	SSB_{F01} /SSB_0	0.35
F_{cur}/ F_{max}	0.29	F_{cur}/ F_{mey}	0.45	F_{cur}/ F_{01}	1.15
Management reference points in the context of recruitment overfishing (Thompson and Bell approach)					
Considering $F_{0.5}$ as a target reference point		Considering $F_{0.4}$ as a target reference point		Considering $F_{0.3}$ as a target reference point	
$F_{0.5}$ (yr^{-1})	2.96	$F_{0.4}$ (yr^{-1})	2.88	$F_{0.3}$ (yr^{-1})	4.44
Rel_F_{05} (times)	0.72	Rel_F_{04} (times)	0.70	Rel_F_{03} (times)	1.08
Y_{05} (t)	2204.96	Y_{04} (t)	2185.40	Y_{03} (t)	2441.74
R_{05} (Million ₹)	388.02	R_{04} (Million ₹)	384.96	R_{03} (Million ₹)	422.95
B_{05} (t)	1246.75	B_{04} (t)	1261.53	B_{03} (t)	1046.85
SSB_{05} (t)	706.31	SSB_{04} (t)	718.62	SSB_{03} (t	543.13
Y_{cur}/ Y_{05}	1.09	Y_{cur}/ Y_{04}	1.10	Y_{cur}/ Y_{03}	0.98
B_{cur}/ B_{05}	0.87	B_{cur}/ B_{04}	0.86	B_{cur}/ B_{03}	1.03
B_{05} /B_0	50.00	B_{04} /B_0	0.51	B_{03} /B_0	0.42
SSB_{cur}/ SSB_{05}	0.81	SSB_{cur}/ SSB_{04}	0.80	SSB_{cur}/ SSB_{03}	1.05
SSB_{05}/SSB_0	39.17	SSB_{04}/SSB_0	0.40	SSB_{03}/SSB_0	0.30
F_{cur}/ F_{05}	1.39	F_{cur}/ F_{04}	1.43	F_{cur}/ F_{03}	0.92

L_{∞}: Asymptotic length; K: Growth co-efficient; t_0: Age at zero length; φ': Growth performance index; t_{max}: Longevity of the fish; M: Natural mortality rate; F: Fishing mortality rate; Z: Total mortality rate and E: Exploitation rate; L_{opt}: Length at which the biomass of cohort is at maximum; L_{c_opt}: Length of capture that maximises catch from a cohort; L_{C50}, L_{C75} and L_{C95} respectively are the lengths at which the 50, 75 and 95% of the fishes that encounters the gear are caught; t_{C50}, t_{C75} and t_{C95} respectively are the ages at which the 50, 75 and 95% of the fishes that encounters the gear are caught; L_{m50}, L_{m75} and L_{m95} respectively are the lengths at which the 50, 75 and 95% of the fishes in a stock mature; t_{m50}, t_{m75} and t_{m95} respectively are the ages at which the 50, 75 and 95% of the fishes in a stock mature; Y_{cur} and Y_{max} are the current and maximum yield respectively; R_{cur} and R_{max} are the current and maximum revenue respectively; B_0, B_{cur} and B_{msy} are the initial biomass, current biomass and the biomass required to produce MSY respectively; SSB_0, SSB_{cur} and SSB_{max} are the initial spawning stock biomass, current spawning stock biomass and the spawning stock biomass required to produce MSY respectively; F_{05}: is the fishing mortality at which B/B_0=0.50; F_{04}: is the fishing mortality at which SSB/SSB_0=0.40 and F_{03}: is the fishing mortality at which SSB/SSB_0=0.30; NA: Not available.

Table 2. A comparative summary of the earlier reports on life history characteristics of *P. stylifera*

Sex	L_∞ (mm)	K (yr^{-1})	t_0 (yr)	φ'	M (yr^{-1})	Location	Reference
Male	125.70	1.47	0.133	2.37	NA	Ambalapuzha, India	Kurup and Rao (1974)
Female	130.10	1.67	0.121	2.45	NA		
Male	113.80	1.92	0.239	2.40	NA	Mangalore, India	Ramamurthy (1980)
Female	132.70	1.32	0.124	2.37	NA		
Male	99.20	2.38	0.060	NA	NA	Goa, India	Achuthankutty and Parulekar (1986)
Female	139.70	1.08	0.021	NA	NA		
Male	129.72	2.23	NA	2.57	2.28	Cochin waters, India	Alagaraja *et al.* (1986)
Female	134.38	2.45	NA	2.65	2.40		
Male	108.00	1.19	NA	2.14	2.61	Cochin, India	Suseelan and Rajan (1989)
Female	135.00	1.05	NA	2.28	2.26		
Male	119.20	1.45	NA	2.31	2.96	Maharashtra, India	Chakraborty *et al.* (1994)
Female	140.80	2.15	NA	2.63	3.60		
Male	138.21	1.89	0.034	2.56	NA	Mangalore, India	Anantha *et al.* (1997)
Female	161.86	1.76	0.017	2.66	NA		
Male	111.80	2.48	-0.033	2.49	2.70	Calicut, India	Sarada (2002)
Female	132.03	2.29	-0.007	2.60	2.50		
Male	120.00	1.59	-0.0004	2.36	NA	Saurashtra, India	Dineshbabu (2005)
Female	147.00	1.41	-0.0014	2.48	NA		
Male	117.00	1.25	NA	NA	1.39	Kerala, India	Pillai *et al.* (2021)
Female	131.00	1.10	NA	NA	1.24		
Male	31.50^{CL} 141.99^{TL}	1.23	NA	2.39*	2.32	Kuwait	Mathews *et al.* (1987)
Female	35.00^{CL} 145.05^{TL}	1.23	NA	2.41*	2.71		
Male	26.90^{CL} 121.91^{TL}	1.33	0.03	(2.98) 2.30*	2.00	Kuwait	Mohammed *et al.* (1998)
Female	36.80^{CL} 151.93^{TL}	1.46	0.32	(3.29) 2.53*	2.41		
Male	21.00^{CL} 96.15^{TL}	1.10	-0.159	(2.69) 2.01*	2.05	Qeshm Island, Iran	Safaie (2017)
Female	27.00^{CL} 114.46^{TL}	1.20	-0.135	(2.94) 2.20*	2.23		
Male	54.60^{CL} 242.86^{TL}	1.24	-0.013	(1.57) 2.86*	1.77	Teluk Penyu, Indonesia	Suradi *et al.* (2017)
Female	65.08^{CL} 260.16^{TL}	1.11	-0.028	(1.67) 2.88*	1.56		
Sex pooled	142.60	1.77	-0.001	2.56	3.00	West Bengal, India	Present study

L_∞: Asymptotic total length; K: Growth co-efficient; t_0: Age at zero length; φ': Growth performance index; M: Natural mortality; mm: Millimeter and yr: Year; L_∞ values with CL superscript: Asymptotic carapace length; L_∞ values with TL superscript: Asymptotic total length calculated using asymptotic carapace length using the relationship between CL and TL given by Mohammed *et al*. (1998); φ' values in bracket are the authors values from the study and values with an asterisk superscript are values recalculated using the formulae $ø' = \log_{10}K + 2\log_{10} L_\infty$ (Pauly and Munro, 1984); NA: Not available.

for the estimation of φ'. The lower φ' reported from Indonesian waters (Suradi *et al*., 2017) is also doubtful, as the CL_∞ used for the estimation of φ' is unreasonably higher (54.6 cm for males and 65.08 cm for females), which may not be achievable by the species. The growth performance index (φ) obtained in the present study is found to be in the reasonable range (2<φ<3) recommended within the same family (Pauly and Munro, 1984).

The age at which the length of the individual is theoretically zero (t_o, which can also be used as a proxy for hatching time) derived using 0.27 mm as the mean total length of Nauplius-1 (L_0) was about -0.0011 yr (*i.e.,* about 10 h), which is slightly shorter than the earlier report where the hatching time for the species has directly been observed to vary from 15 to 16 h at 25.6-27.7^{0}C water temperature (Muthu *et al*., 1978). However, the t_o reported in this study is drastically shorter compared to the earlier reported t_o for the species, which varies from -0.007 yr (about 61 h by Sarada, 2002) to 0.239 yr (about 2094 h by Ramamurthy, 1980). The relatively high estimates of t_0 reported in earlier studies require revalidation in light of the shorter embryonic development period of the species documented by Muthu *et al*. (1978). Since the length at birth (L_0) is always a positive number, the 't_o' can never be a positive number. The extrapolated growth curve with a positive y-intercept (L_0) will invariably have a negative x-intercept (t_o). A growth curve with a positive x-intercept (t_o) when extrapolated will have a negative y-intercept at length at birth L_0 (length at birth), which is impossible. Therefore, the positive 't_o' values reported by Kurup and Rao (1974), Ramamurthy (1980), Achuthankutty and Parulekar (1986), Anantha *et al*. (1997) and Mohammed *et al*. (1998) deserve a recalculation and validation.

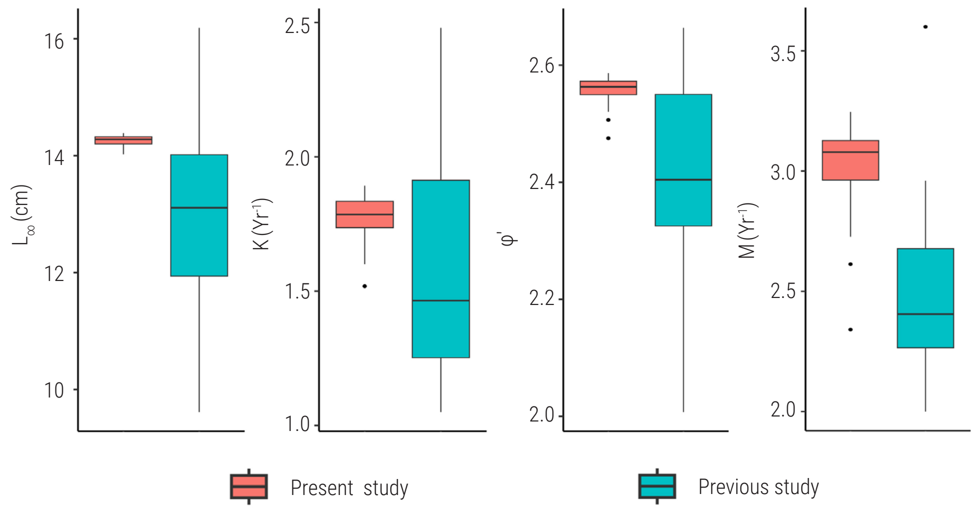

Fig. 2. Comparison of von Bertalanffy's growth parameters and natural mortality rate of *P. stylifera* with the earlier studies

In the present study, the longevity (t_{max}) of the shrimp was found to be 1.53 yr (about 18 months), which is more or less the same as the observations of Chakraborty *et al*. (1994), Anantha *et al*. (1997), and Dineshbabu (2005). However, the present t_{max} was shorter compared to the earlier studies, where it was reported to vary from 24 to 30 months (Achuthankutty and Parulekar, 1986; Mathews *et al*., 1987; Suseelan and Rajan, 1989; Geetha and Nair, 1992; Safaie, 2017; Pillai *et al.,* 2021). In some cases, the present t_{max} was also observed to be longer when compared with certain earlier studies, where it has been reported to vary from 14 to 16 months (Alagaraja *et al*., 1986; Sarada, 2002). As the t_{max} is actually the maximum observed age of the species, it should be independently and directly estimated by tagging experiments (Hordyk *et al*., 2015; Then *et al*., 2015). But under a data-poor situation, it is estimated as the longevity of the species assuming 99% of the animals in stock (in the unexploited state) die due to natural causes when they reach L_{max} which is approximately 95% of L_∞ (Alagaraja, 1989; Srinath, 1998; Quinn and Deriso, 1999) and should be shorter for a fast-growing species like *P. stylifera* that attains L_{max} at 93% of L_∞. Since the indirect estimate of t_{max} depends on the growth rate of the individuals, it varies from location to location depending on the growth coefficient (K) estimated for the species.

Length-weight relationship (LWR)

The relationship between total body length (TL) and body weight (BW) is shown in Fig. 3 and given below:

Male: BW= 0.004 (TL) $^{3.17}$ (Adjusted R^2=0.99, p-value: < 2.2×10^{-16})

Female: BW= 0.008 (TL) $^{2.91}$ (Adjusted R^2=0.96, p-value: < 2.2×10^{-16})

Combined: BW= 0.006 (TL) $^{3.04}$ (Adjusted R^2=0.96, p-value: < 2.2×10^{-16})

where, W is the body weight in g and TL is the total body length in cm. The exponent (b) was significantly lower (F = 4.23, p = 0.04), but the intercept was significantly higher (F = 30.94, p≤4.4 × 10^{-8}) in females compared to male shrimps. It was observed that the females are heavier compared to the males of the same size. However, the growth was negatively allometric (b<3, F-value = 36.87, p = 1.23 × 10^{-9}) in females compared to males, where it was positively allometric (b>3, Fvalue = 6.11, p = 0.01). This agrees well with the observations of Mane *et al*. (2019), who found that females, while usually bulkier than males, also possess a comparatively longer rostrum that grew faster, as a result of which it could not gain weight proportionately to its length increments and thereby show a negatively allometric growth. Similarly, there are earlier studies in which females have been observed to be heavier compared to males (Suseelan and Rajan, 1989; Safai, 2017; Suradi *et al*., 2017). Contrary to this, there are also studies where the males were observed to be heavier compared to the females (Achuthankutty and Parulekar, 1986; Mohammed *et al*., 1998; Sarada, 2002). However, growth was observed to be isometric when sex combined weight at length data

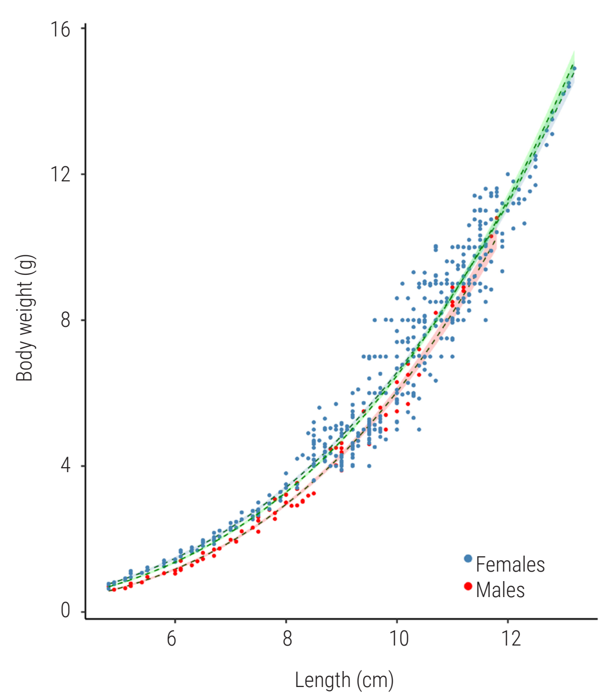

Fig. 3. Length-weight relationship of *P. stylifera* in West Bengal waters

was used, as the slope (b) did not vary significantly (F value = 3.63, p = 0.06) from the theoretic value of 3 and the same has been used in the study for the assessment of the stock status of the species.

Mortality and exploitation

The natural mortality rate (M) could be defined as the instantaneous rate of population decay on an annual basis due to fisheries-independent factors such as predation, starvation, disease and senescence. Once the fish are recruited to the fishery, the M acts continuously and simultaneously with fishing mortality (F) to determine the annual survival (exp[-(M+F)]) of the stock. M is one of the most important parameters that critically influence the outcome of fisheries stock assessment. Nevertheless, it is also the most difficult parameter to estimate due to a dearth of unbiased tagging data or age-composition data in the absence of fishing (Maunder *et al*., 2023). There is evidence that suggests that M varies over time, age and sex of the species (Lorenzen, 1996; Gislason *et al*., 2010); yet, for ease of analysis and modeling simplicity, a constant M is usually assumed for a stock (Deroba and Schueller, 2013; Johnson *et al*., 2015). For any given stock, estimating M is quite challenging, as there are many methods with their own advantages and disadvantages. M, calculated from general empirical relationships based on life history theory, has been well reviewed by Then *et al*. (2015) and Maunder *et al*. (2023). In the present study, a simple approach based on life history theory has been used for the estimation of M. The approach simply assumes that 99% of the fish in an unexploited stock die due to only natural causes when they reach L_{max} (which is approximately 93.4% of the L_∞ for *P. stylifera*), which results in an overall survival of 1% at t_{max} (Alagaraja, 1989; Srinath, 1998; Quinn and Deriso, 1999). Thus, in the absence of fishing mortality (Z = M), by assuming 1% survival (p = 0.01) at t_{max} and rearranging the equation for survival [$p = N_t/N_0 = \exp(-M * t_{max})$], the M can be easily estimated using the relationship, $M = -\ln(0.01)/t_{max}$ which is equal to 3.0 yr^{-1}. Though the survival (p) at t_{max} is usually assumed to be between 1 to 5% (Hewitt and Hoenig, 2005), with empirical work suggesting a p-value of 1.5% to be more appropriate (Hewitt and Hoenig, 2005), how much actual survival is to be expected at t_{max} for the species under investigation is quite subjective in nature and depends mainly on the good estimation of life history characteristics (t_{max}) of the species (Hordyk *et al*., 2015). In the present study, for simplicity of calculation, a survival of 1% (p = 0.01) was assumed at t_{max}, which gave an M of 3.0 yr^{-1} and an M/K ratio of 1.7, which is slightly higher compared to BH-LHI.

According to the bio-energetic modelling by Jensen (1996), the optimal value for the M/K ratio has been suggested as 1.5, which with $L_m/L_\infty = 0.66$ and $M \times T_m = 1.65$ is popularly considered BH-LHI as empirical works suggest that the ratio is relatively consistent between closely related stocks (Beverton, 1992; Charnov, 1993). Despite, the recent studies that have revealed the variability in the M/K ratio from BH-LHI (Frisk *et al*., 2001; Prince *et al*., 2015), the ratio is broadly assumed to be invariant due to its usefulness in stock assessment studies (Hordyk *et al*., 2015; Froese *et al*., 2018). A typical M/K value of 1.5 indicates that the species grows throughout its life, reaching maximum size at maximum age. But a species with an M/K value less than BH-LHI (<1.5, which is usually observed in slow-growing K-selected species) grows faster initially to attain maximum size quite early in life while the number of individuals in the cohort is still high, after which it lives for a longer period with no apparent body growth (Hordyk *et al*., 2015). In the case of such species, the stock attains its maximum biomass at an early age, predominantly constituted by larger individuals, after which it declines rapidly due to the mortality of fully grown individuals. Contrary to this, a species with a higher M/K value (>1.5), which is usually observed in fast-growing r-selected species, grows relatively faster throughout its entire life and reaches maximum size near maximum age (Hordyk *et al*., 2015). As a result, the stock of such species attains maximum biomass at a relatively older age when the individuals of the stock are still small and growing. Therefore, the M/K ratios of species greatly influence the biomass and yield trajectory under similar exploitation conditions (Hordyk *et al*., 2015).

The other mortality parameters (*i.e.,* F and Z) and exploitation parameters (E) of sex-combined data are shown in Table 1 and Fig. 4. The total biomass of a cohort is a dome-shaped function of age, which is shown in Fig. 5. The length at which the biomass of a cohort is at its maximum (L_{opt}) can be easily estimated for a species that follows BH-LHI using the empirical relationship between the life history characteristics of the species. The L_{opt} obtained following Holt (1958) and Beverton (1992) was found to be 9.11 cm TL. According to Holt (1958), the maximum possible yield could be attained if the entire cohort could be harvested immediately when it reaches t_{opt} (*i.e.,* 0.57 yr, age corresponding to L_{opt}). Contrary to the empirical estimates, the length-based cohort analysis (Lcohor) of the sex-combined data showed that the cohort attains the maximum biomass when it attains 8.0 cm TL (L_{opt_Lcohor}) corresponding to an age of 0.47 yr (t_{opt_Lcohor}). The Lcohor also revealed that at L_{opt}, the F (1.94 yr^{-1}) was still lower than the M (3.00 yr^{-1}) (Fig. 5). The F exceeded M only when the shrimp attained 9.0 cm TL (Fig. 5). Being an r-selected species with a high growth rate and short lifespan, *P. stylifera* suffers tremendous mortality

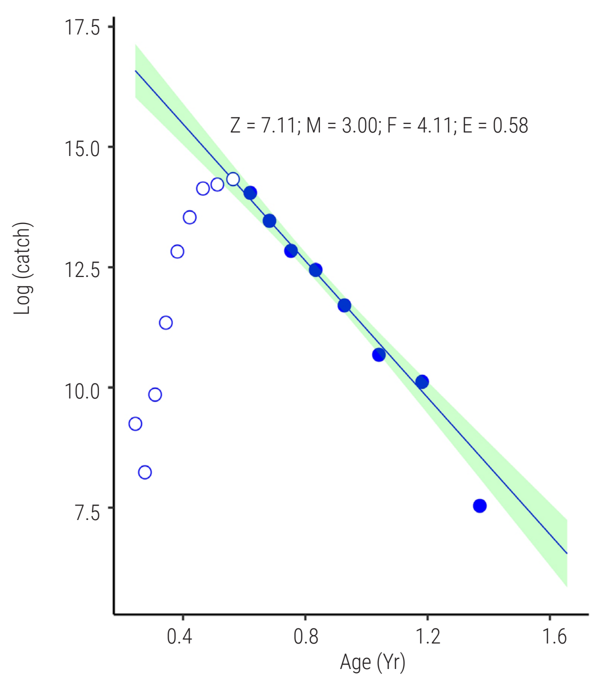

Fig. 4. Estimation of mortality and exploitation parameters of *P. stylifera* from the Length-converted catch curve method

due to natural causes, which alone is capable of decimating the cohort by nearly 95% just within one year. Therefore, the stock of the species could be subjected to higher exploitation to improve the yield, which otherwise would simply perish due to higher mortality from natural causes. Furthermore, the entire cohort under the prevalent F of 4.11 yr^{-1} would reduce to 1% of its initial population strength just within 0.65 yr (approximately 8 months). However, considering the short generation time (t_g, *i.e.,* the average age of parents at the time their young are born) of 0.48 yr (approximately 6 months by assuming $t_g = t_{m50} = t_{opt\_Lcohor}$), the prevalent exploitation level (E_{cur} = 0.58) would allow the stock to reproduce. Therefore, the prevalent exploitation could be allowed with strict monitoring of the spawning stock biomass (SSB) so that it is maintained above the minimum critical level for healthy recruitment.

Selectivity, maturity and spawning

The length at recruitment (L_r) for *P. stylifera* was 4.3 cm (TL). The empirical estimate of length at capture (L_{c_opt}) that ensures the maximum biomass of catch under the prevalent fishing mortality of 4.11 yr^{-1} was calculated to be 7.83 cm. However, the L_{c_opt} derived using the precise estimate of L_{opt_Lcohor} (*i.e.,* 8.0 cm) from Lcohor was 6.98 cm ($L_{c\_opt\_Lcohor}$). On the other hand, the length at capture (L_{c50}) derived by performing logistic regression of probability of captures of sequential length classes using trawl type selection was 8.16 cm (Fig. 6), which is 1.18 cm higher compared to the $L_{c\_opt\_Lcohor}$. This implies that there is still scope to further decrease the length at capture, which can improve the yield from the stock.

The maturity study revealed that the size at first maturity (*i.e.,* the minimum size at maturity) was 6.7 cm, but 50% of the shrimps in stock became mature (L_{m50}) at a TL of 8.15 cm and 0.48 yr of age (t_{m50}) (Fig. 7). *P. stylifera* has been recorded to start maturing (size at first maturity) at a minimum TL of 6.3 cm in Cochin (Rao, 1968), 6.5-6.8 cm in Kerala (Pillai *et al.,* 2021), 7.0 cm in Cochin (George *et al.*, 1968), 7.1 cm in Mangalore (Ramamurthy, 1980), 7.5 cm in Malabar (Menon, 1953) and 7.6 cm in Mumbai (Kagwade, 1980) coasts. The length at maturity (L_{m50}) observed in the present study can be compared with the earlier studies, where L_{m50} has been reported to vary from 7.1 cm in Kerala (Pillai

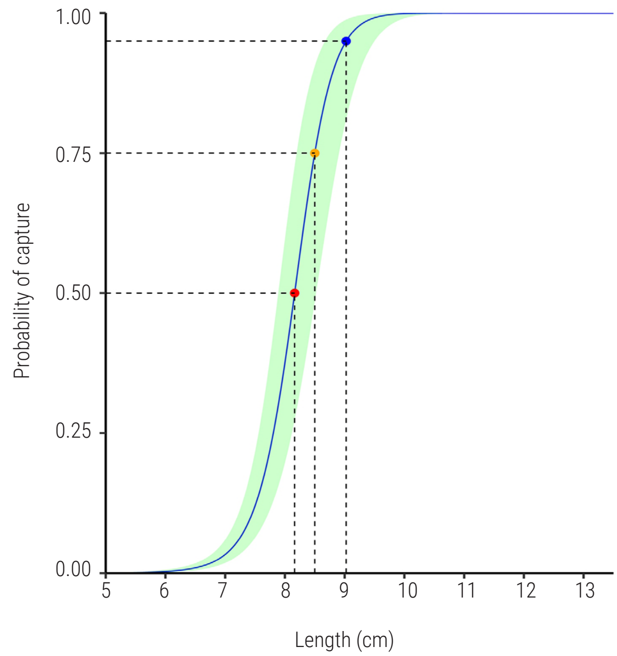

Fig. 6. Length at capture (L_{c50}) of *P. stylifera* in the West Bengal waters

et al., 2021), 7.5 cm in Calicut (Sarada, 2002), Cochin (Geetha and Nair, 1992) and 9.3 cm in Saurashtra (Dineshbabu, 2005) coasts, to as large as 10.55 cm reported from Mumbai waters (Kagwade, 1980). The mature specimen of the shrimp was observed throughout the year, which indicates that the species is a protracted continuous spawner with major spawning events during April-June and October-December. The finding agrees well with the earlier observations by Rao (1968), Kurup and Rao (1974), Ramamurthy (1980) and Geetha and Nair (1992).

The age at maturity estimated by fitting the growth model of the shrimp revealed that 50% of the shrimps in the stock mature in about 6 months (t_{m50} ≈ 0.48 yr), at which point it also enters into the peak phase of exploitation (t_{c50} ≈ 0.48 yr) which is also coinciding

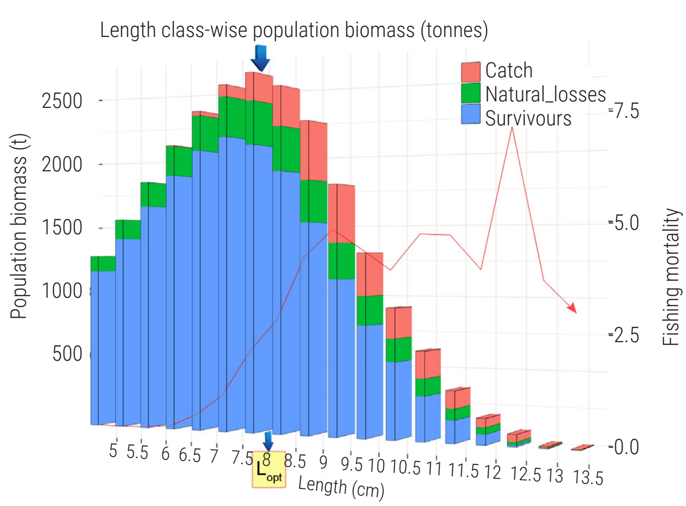

Fig. 5. Length structured cohort analysis (Lcohor) of *P. stylifera* from West Bengal waters

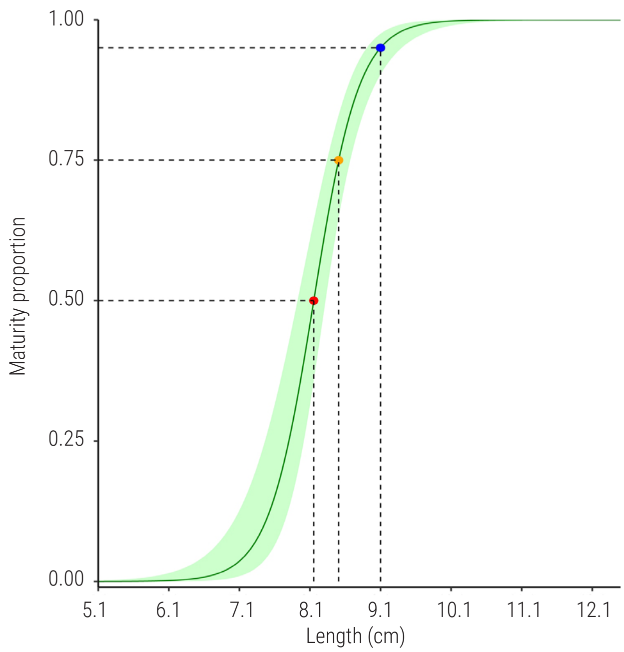

Fig. 7. Size at maturity (LM_{50}) of *P. stylifera* (female) in the West Bengal waters

with the L_{cohor} suggested t_{opt} for the cohort. As egg production is proportional to biomass, L_{opt} is also considered the optimal strategy zone for maturation (L_{m50}) that maximises the evolutionary fitness of a species (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992).

The L_{m50} for *P. stylifera* derived by logistic regression in the present study is producing an L_{m50}/L_{∞} ratio of 0.57, which is lower compared to the ideal ratio of 0.66 expected from a species that confirms BH-LHI (Hordyk *et al*., 2015; Prince *et al*., 2015). This indicates that the species matures early at a smaller size. The faster growth rate (K), high natural mortality (M) and smaller longevity (t_{max}) effectively shorten the adult life span for *P. stylifera* and therefore, the species matures early to ensure its continuity through fast reproduction (Beverton, 1992). The derived t_{m50} (*i.e.,* 0.48 yr), t_{m50}/t_{max} (*i.e.,* 0.31) and L_{m50}/L_{∞} ratio of 0.57 indicate that *P. stylifera* starts its adult (reproductively active) life both at a younger stage and at a smaller size compared to the species that confirms BHLHI to maximise its recruitment. The high M/K as well as low t_{m50}/t_{max} and L_{m50}/L_{∞} ratios qualify the species to be considered "r-strategists" (Pianka, 1970) or "opportunistic-strategists" (King and McFarlane, 2003) with shorter generation time that maximises its intrinsic rate of population growth and turnover. However, due to its shorter generation time, *P. stylifera*, like any other opportunistic strategist, is also highly vulnerable to environmental conditions for the success of recruitment and therefore, fluctuations in environmental conditions could greatly impact the biomass. Therefore, such strategists require frequent assessment on an annual or biannual basis to ensure a critical minimum spawning stock biomass (SSB) is maintained for the long-term sustainability of the species (King and McFarlane, 2003).

Stock status assessment

The BSM, being a surplus production model, ignores the age, size and sex-specific variations in the life history characteristics of individuals in stock and pools the overall effects of recruitment, growth and mortality (all aspects of production) of the undifferentiated biomass into a single production function (Hilborn and Walters, 1992). Though often used in data-poor situations to provide a coarse estimate of MSY and F_{msy}, the methodology could complement the data-moderate and data-rich approaches, especially to reconstruct the possible abundance and exploitation trajectories for the population over a longer time frame.

Therefore, an initial estimate on the depletion status (B/k), biomass status (B/B_{msy}), exploitation status (F/F_{msy}) and management reference points (*i.e.,* MSY, B_{msy} and F_{msy}) for *P. stylifera* was derived by the implementation of the Bayesian Schaefer surplus production model (BSM) using the catch and abundance data (CPUH, *i.e.*, catch per unit hour) during the period 2007 to 2021 and prior knowledge on the resilience and depletion status of the species, which are presented in Table 1 and Fig. 8. The analysis revealed that the current biomass (B_{cur}) is not only at a high level (B_{cur}/k = 0.58) compared to the initial level (k) of 10.8 thousand t but also 15% higher (B_{cur}/B_{msy} = 1.15; Table 1; Fig. 8a) than what is actually required to produce MSY of 3.01 thousand t and therefore could be considered safe for ensuring the sustainability of the resource. Furthermore, the current catch (Catch/ MSY = 0.99, Table 1; Fig. 8b) and fishing mortality rate (F_{cur}/F_{msy} = 0.85, Table 1; Fig. 8d) were found to be lower by 1 and 15% respectively, compared to the MSY levels, and therefore, there is still scope to marginally increase the exploitation level. However, as the confidence intervals for these ratios (B_{cur}/B_{msy}: 0.58-1.92; F_{cur}/F_{msy}: 0.42–2.23) include values that cross precautionary thresholds, it is recommended to follow a precautionary approach with regular monitoring of spawning stock biomass and adaptive harvest control rules. The Kobe plot (Fig. 8c) revealed that there is a high probability (57.9%) that the stock in the final year of assessment (*i.e.,* 2021) was in the green zone, which indicates that the stock biomass and fishing pressure are healthy and sustainable. The Kobe plot also provided insight into the long-term performance of the stock, where it could be seen that the stock was in a rebuilding phase (yellow zone) for almost a decade from 2007 to 2016, during which the gradual decrease in targeted fishing pressure would have helped in the revival of stock biomass to a healthy and sustainable level (green zone).

Consequent to the long-term analysis, a micro-analytical approach (length-based Thompson and Bell dynamic pool model) was also followed to get a better understanding of the stock status of *P. stylifera* using high-resolution information such as age or length group-wise life history and exploitation parameters. The effects of changes in fishing pressure (keeping L_{c50} at the current level, *i.e.,* 8.16 cm) as well as the combined effect of changes in both fishing pressure and selectivity (L_{c50}) on the yield and spawning stock biomass (SSB) are shown in Fig. 9 and 10a, b), respectively. The analysis revealed that current fishing mortality needs to be increased by 3.42 times (F_{max} = 14.05 yr^{-1}, F-multiplier = 3.42 times) to maximise the yield to 2673.02 t from the current level of 2403.59 t (Table 1, Fig. 9). However, such an increase in fishing effort may not be efficient, as the yield would increase only by 11.21% despite a 241.85% increase in fishing mortality rate, which will also drastically deplete the SSB to 14.36% levels (Fig. 9). Interestingly, the present selectivity (leading to an L_{c50} of 8.16 cm) is well within the selectivity range (L_{c50} that ranges from 7.7 to 9.7 cm) that will produce the highest yield isopleth band (with a yield of about 2600 t) if the exploitation intensity is increased to the F_{max} (Fig. 10a). However, as mentioned above, without any change in current selectivity, the

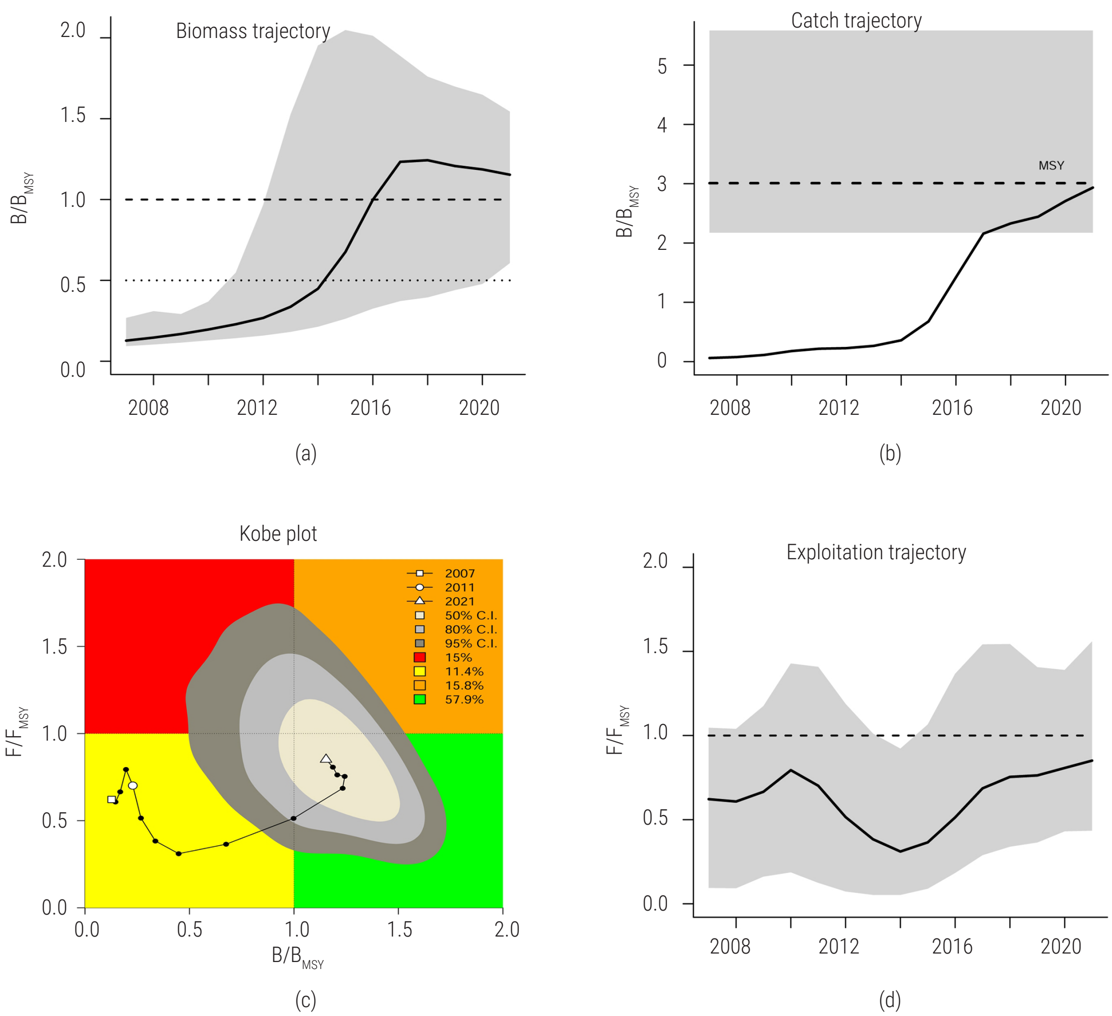

Fig. 8. Relative stock biomass and exploitation status of *P. stylifera* in the West Bengal waters derived through BSM approach

SSB will drastically decline to 14.36% with such high exploitation intensity (F_{max}). Therefore, to maintain a safer SSB of 30% under such a high F_{max}, the gear selectivity needs to be increased so that L_{c50} will be above 9.5 cm (Fig. 10b).

In data-moderate situations, especially when it is not possible to define the relationship between spawning stock biomass and recruitment (SSBR), the reference point, *i.e.,* F_{max} obtained from the dynamic pool models, is used as a proxy for F_{msy}. Nevertheless, the F_{max} obtained from the Thompson and Bell model often tends to overestimate the F_{msy} as it does not account for the reduction in recruitment that would eventually occur due to a reduction in SSB. Due to this limitation and the considerable uncertainties involved in the assessment of life history and exploitation parameters, it is necessary to use precautionary management reference points (Rosenberg and Repestro, 1996). As a precautionary approach, a further lower fishing mortality indicator corresponding to 10% of the slope of the yield curve at the origin (*i.e.,* $F_{0.1}$) has been recommended to be used as a biologically precautionary target reference point instead of F_{max} (Gulland and Boerema, 1973). Therefore, following $F_{0.1}$, the fishing mortality in the present study should be reduced by 13% ($F_{0.1}$ = 3.58 yr^{-1}, F-multiplier = 0.87 times), which will maintain the B and SSB at healthier 46% and 35% levels, respectively (Fig. 9). Unlike F_{max}, the $F_{0.1}$, which is considered as conservative or cautious reference point, often underestimate F_{msy}. The point to be noted here is that, just like the F_{max}, the $F_{0.1}$ also does not give any consideration to the B and SSB of the stock and therefore should not be used in the context of recruitment overfishing. Therefore, both the F_{max} and $F_{0.1}$ are used as management reference points in the context of growth overfishing, the latter being a precautionary and conservative indicator.

In addition to the above management reference points, another class of indicator used in the context of recruitment overfishing is the spawning potential ratio (SPR). As an increase in fishing mortality rates negatively influences the survival of recruits in a cohort, it inversely affects the lifetime spawning potential of recruits in a cohort (Goodyear, 1993). This reduction in the lifetime spawning potential of recruits at a given level of fishing mortality rate (F) is usually expressed as a ratio popularly known as the spawning potential ratio (SPR) that depicts the percentage decrease in the spawning potential compared to that of a virgin stock when F = 0 and therefore, the relative spawning stock biomass (SSB/SSB_0) is also used as a proxy for SPR. The corresponding F that reduces the SPR to a certain percentage (%SPR) is referred to as F%SPR and can be used as a proxy for the biological reference point in the context of recruitment overfishing (Mace and Sissenwine, 1993). Usually, F%SPR that reduces the spawning potential (here, SSB) to a level that ranges from 20% (*i.e.,* F0.2) to 30% (*i.e.,* F0.3) of virgin spawning potential (SSB_0) has frequently been used to define recruitment overfishing (Mace and Sissenwine, 1993; Rosenberg and Repestro, 1996). Goodyear (1993) has advocated an SSB level of at least 20% unless there is evidence of exceptionally strong density dependence. According to Clark (1991; 1993), the fishing mortality rate that reduces a recruit's lifetime reproductive potential (SPR) to 35-40% relative to unexploited conditions (*i.e.,* F0.35 to F0.4) could be used as a conservative proxy for F_{msy}. If there is considerable uncertainty, then instead of using proxies like F_{max} and $F_{0.1}$, it is advisable to use fishing mortality rates of F0.30 (for the highly resilient species), F0.35 (for the average resilient species) and F0.40 (for the low to moderate resilient species) as the general default proxies for F_{msy} (Gabriel and Mace, 1999).

In another publication, Clark (2002) recommended a SPR of 35-40% or even less for the short-lived species with high resilience, whereas the long-lived stocks with low resiliency (steepness<0.67) would require a higher SPR as 50%–60% or more. In the present data-moderate situation, considering the high resilience of the species, an SPR of 30% could be considered a relatively safe biological reference point in the context of recruitment overfishing. Furthermore, as the length of maturity is almost the same as the length at capture ($L_{m50} \leq L_{c50}$) in the current fishery, the SPR of the stock could be expected to decline at a slower rate even at relatively higher fishing mortality, as a result of which such a stock is capable of maintaining a higher SPR of 40% even at high F/M ≥ 1.0 (Hordyk

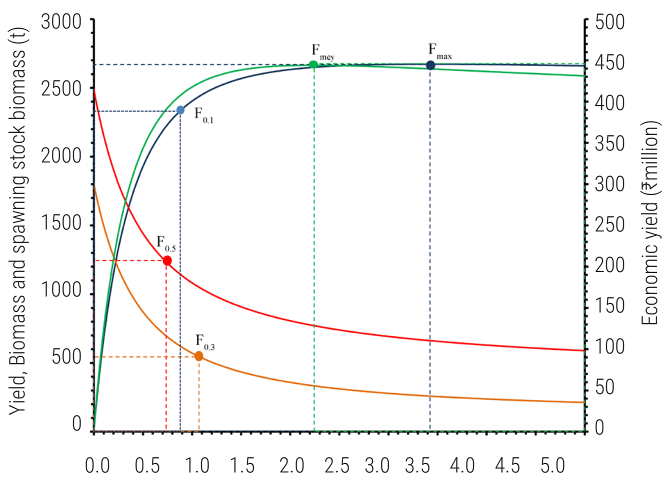

Fig. 9. 2D projection of changes in yield (Y), revenue (R), biomass (B) and spawning stock biomass (SSB) in response to the changes in fishing effort (F)

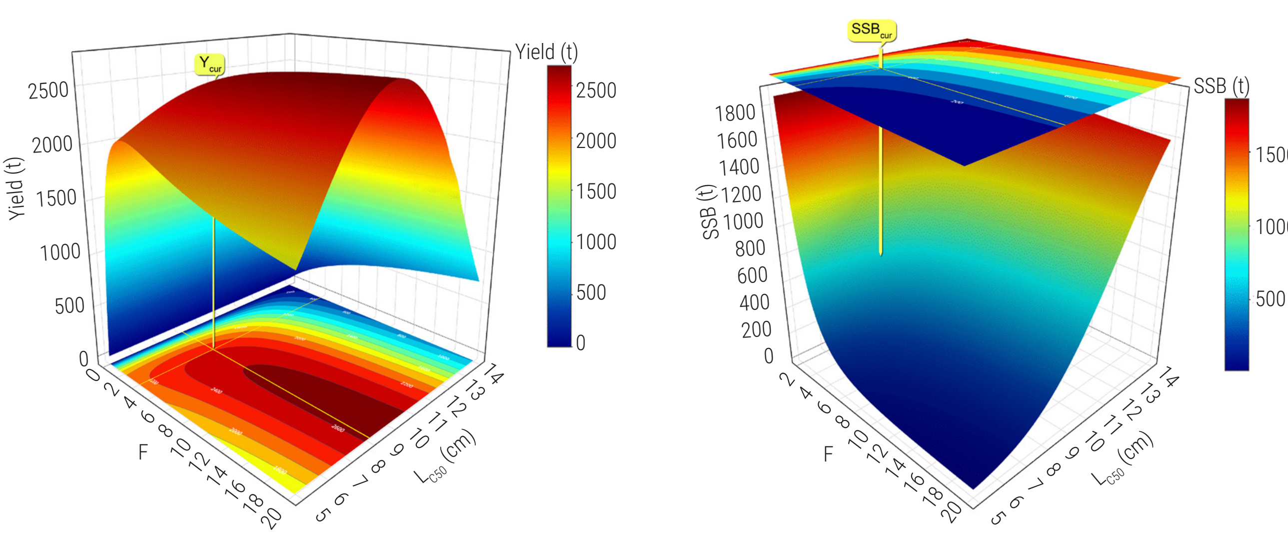

Fig. 10. 3D projection of change in yield in response to the combined changes in fishing effort (F) and selectivity (L_{c50}) projected above the yield isopleths derived

et al., 2015). Therefore, considering $F_{0.3}$ as a precautionary proxy for F_{msy}, there is still scope to further increase the fishing mortality by a mild 8% (F_{max} = 4.44 yr^{-1}, F-multiplier = 1.08 times), which would marginally increase the yield by 1.59% (Sustainable yield = 2441.74 t) and revenue by 1.26% (Sustainable revenue = ₹422.95 million) from the current levels while maintaining the B and SSB at a safer 42 and 30%, respectively, compared to the virgin stock levels (Table 1; Fig. 9). Further, it must be emphasised that, as the species is a "r-strategist" with a shorter generation time, it is also highly vulnerable to environmental fluctuations for the success of its recruitment. Therefore, frequent assessment on an annual or biannual basis is highly essential to maintain the critical minimum SSB of 30% or higher for ensuring the long-term sustainability of the species (King and McFarlane, 2003).

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