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Diel and Tidal Variations of Larvae and Juveniles of *Metapenaeus dobsoni* from Sundarbans Estuarine System, India

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Abstract
The Sundarbans Estuarine System (SES) is a mangrove dominated monsoonal, macrotidal estuarine system in the east coast of India and is one of the best nursery grounds for shellfish populations in this region. The early developmental stages of penaeid prawns prefer the estuaries to complete their bipartite lifecycle. The present study, conducted within the extremely difficult and challenging environment of the SES, is a pioneering attempt to decipher the probable diel and selective tidal variation patterns of different stages (mysis, decapodite and juvenile) of *Metapenaeus dobsoni* in the SES, India. The observations were conducted by selecting a time series sampling protocol of 72 hours each, during the spring and neap phases of the tidal cycle in the peak monsoon month of August 2014. During the spring and neap tides, the total population was observed to be dominated by juveniles (83%) and mysis larva (61%) respectively. The maximum abundance was observed to occur during the night time of the neap phase irrespective of tidal amplitude. During the spring phase the maximum abundance was recorded at low tide conditions irrespective of the diel variations. The increase in the abundance of mysis stages always synchronized with low tides during the neap phase whereas, the peak increase of juvenile abundance synchronized with the ebb currents (low tides) during the spring phase. *M. dobsoni* utilize the tidal currents for their ingress and egress mechanisms in order to travel horizontal distances or remain in their preferred habitats. Our study corroborated the significant importance of ontogenetic diel and a tidal variation of larval and juvenile's abundance in the water column at SES. Such studies of the larval dynamics are very essential in the SES for estimating the fishery potential and sustainable management of wild seed collections by the local fishermen community.

Keywords Sundarbans · *Metapenaeus dobsoni* · Diel variation · Tidal variation · Juveniles · Monsoon

Introduction

Most of the coastal and estuarine benthic species have bipartite life cycles, having one larval or planktonic phase and one benthic phase. Tropical penaeid shrimps, which contribute significantly to the Indian marine fisheries, are highly fecund species with complex life cycles and variable recruitment patterns. Females usually lay eggs in the offshore saline environment; the early larval stages (mainly nauplius and protozoea) migrate to estuarine brackish water for further development and after maturation the juveniles generally egress towards open sea in their benthic mode of life (Garcia and Le Reste 1981; Dall et al. 1990). At all stages the animals apply different behavioural strategies for successfully migrating to their preferred environment, according to changes in the water flow regime. These early larval populations, with limited swimming ability, complete their ontogenetic migrations between oceanic and estuarine habitat with the help of tidal flow (Gibson 2003). Elicited by tidally associated environmental cues, early larval stages swim in the water column during nocturnal flood tides to ingress into the nursery grounds by exploiting the tidal currents. The Flood Tide Transport (FTT) of penaeid shrimp is a behavioural mechanism for shoreward transport into the estuary, simultaneously their Ebb Tide Transport (ETT) is used for seaward migration after development and maturation (Morgan et al. 1996; Lopez-Duarte and Tankersley 2007; Queiroga and Blanton 2004).

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The Sundarbans, the dense forests of natural mangroves are situated on the southern periphery of the huge Ganga-Brahmaputra-Meghna delta. This deltaic complex, also called the Sundarbans delta, is shared jointly by India (~40%) and Bangladesh (~60%). It covers about 26000 sq kms and is a World Heritage Site (UNESCO 1987) owing to the rich biodiversity present in this area, and serving as nursery ground for about 90% of the aquatic species of the east coast of India. The Indian part lies entirely within the state of West Bengal named as Sundarbans Estuarine System (SES hereafter), situated on the north-east coast of India (Fig. 1) which adjoins the Bay of Bengal (Chatterjee et al. 2013; Goutam et al. 2015).

Chatterjee et al. (2013) (SES 2013 hereafter) were the first to report the characteristics of tidal propagation from SES. This baseline study, which was hitherto lacking for the entire SES, was conducted in a 72 hour (18 – 21 March 2011) observational programme named the Sundarbans Estuarine Programme (SEP 2011 hereafter). All the estuaries in the SES are north – south flowing, funnel shaped, shallow but navigable. Their estuarine character is maintained by the mixing of saline seawater carried inwards by the twice daily tides and the local freshwater runoff resulting from the copious precipitation received during the: a) pre-monsoon thunderstorms that occur regularly during March – May in this region; b) Indian Summer Monsoon (June – September) and c) pre- and post monsoon (October – December).

Mangroves are highly efficient in trapping and recycling nutrients and other necessary chemicals and provide habitats for numerous smaller organisms (Mukherjee and Mathur 2012; Gopal and Chauhan 2006; Ghosh et al. 2015) in their detritus and nutrient rich substrate. In the SES, the physical conditions in these smaller ecosystems are delicately balanced and change almost daily with the semi-diurnal tidal transports of salt, sediments and nutrients. These are extensively used as spawning zones and nurseries by a wide variety of marine species including commercially important varieties such as shrimps, prawns, hilsa, crabs, and other edible crustaceans. The role of mangroves as the nursery grounds has been demonstrated by studies comparing shrimp populations in mangroves and other habitats worldwide (Robertson and Duke 1987). The SES faces anthropogenic perturbations due to the nutrient influx from river discharges during the south-west monsoon (Mukhopadhyay et al. 2006). Generally, penaeid prawns spend a part of their life cycle in estuaries wherein the larval stages enter the estuaries using tidal currents (Goswami and George 1978).

Studies about the abundance and distribution of *Penaeus monodon* have been conducted (Hoq et al. 2001) in the Sundarbans region. However, little information is available about *Metapenaeus dobsoni*, which is another predominant economically important shrimp species from this region. Numerous species of commercial interest are of the genus *Metapenaeus* and they constitute an important part

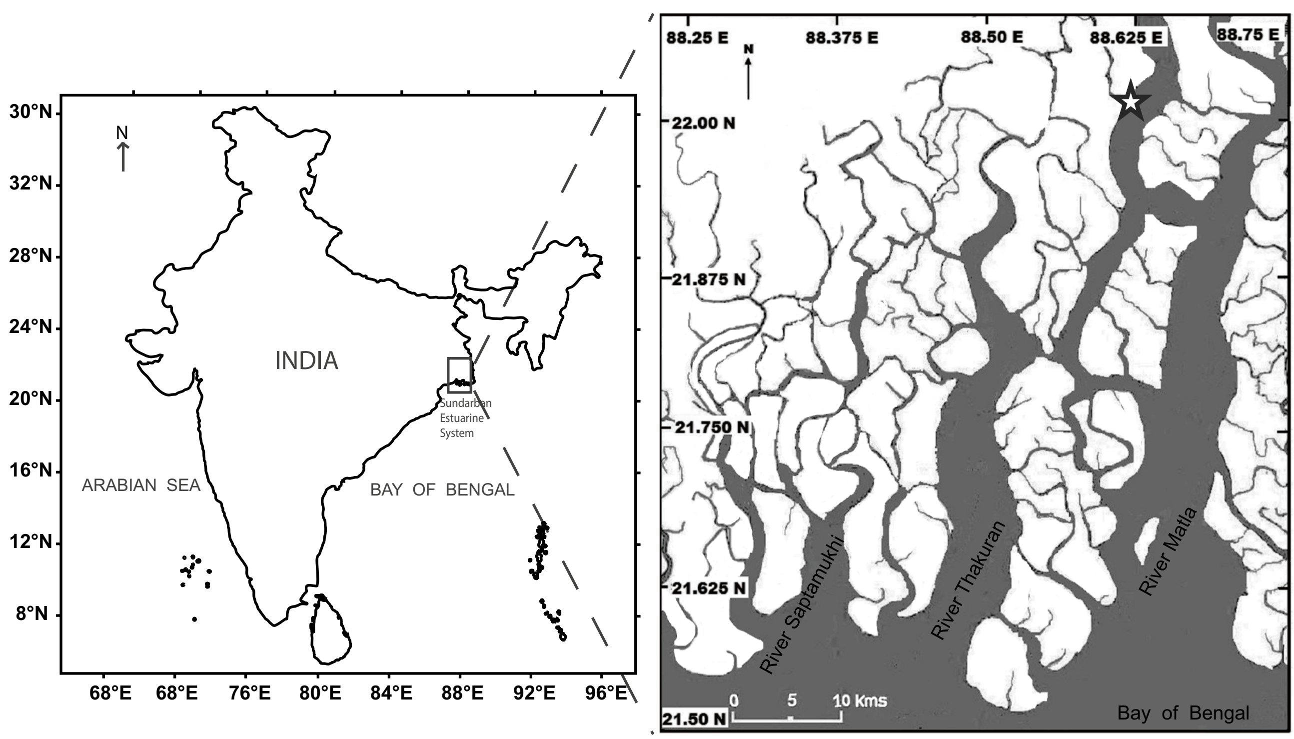

Fig. 1 Map of the study area, star mark indicates the sampling point of the estuary

of fisheries along the Indian coasts. *M. dobsoni* or 'kadal shrimp' as it is more commonly known, is a brackish water, benthic organism found in the tropical waters of India in both the west and east coasts. Their eggs and larval stages are found in the more inshore waters. The embryo of *M. dobsoni* passes through six nauplius, three protozoea and five mysis stages before maturing into decapodites (Muthu et al. 1978) after which they ingress into the brackish waters of estuaries to mature further. Upon reaching the juvenile stage, they return back into the coastal waters and sexual maturity is reached in the sea (Sukumaran et al. 1993).

In the West Bengal coast, penaeid prawn catches contributed utmost (16%) of the total crustacean landings in 2016 (CMFRI 2017). Moreover, the estimated penaeid prawn landing during 2016 was 14895 ton, showing a remarkable increase from the previous year catch of 5897 ton (Mini et al. 2017). Although *Penaeus* sp. has been extensively studied and artificially reared, knowledge about *M. dobsoni* is lacking in spite of its economic importance as it is abundantly found throughout the coasts of India. Nonetheless, to the best of our knowledge, the abundance of different stages of *M. dobsoni* with respect to diel and tidal variations especially during peak monsoon period (July to August) in the SES has hitherto not been investigated.

The present paper describes the occurrence and abundance of different larval stages of *M. dobsoni* during the neap and spring tide phases in the SES in the monsoon period. The aim is to examine the impact of diel and tidal variations on the abundances of different stages of larvae and juveniles of *M. dobsoni* in a tropical mangrove dominated estuarine complex, and the associated environmental factors that can influence their abundances in this estuarine complex. Though the local socio-economic conditions are fully dependent on fishery and various brackish water prawn culture, the identification of the best time as well as tidal period for wild larvae collection in this rural area is very essential. Proper knowledge about the diel and tidal variation of shrimp larval and juveniles' dynamics would be helpful to the local seed (wild shrimp larvae) collectors for a better sustainable fishery development in SES.

Materials and Methods

Study Area and Timing

Kaikhali (22°01'17.09"N/ 88°36'50.7"E), our study station was a selected Time Series Location (TSL) during SEP 2011 and 2014. The choice of Kaikhali as an observational station was also based on our previous knowledge of the behaviour of the tides, salinities and water temperatures. Additionally, the station was selected due to the convenience of transportation and communication, availability of manpower and motorboats (which are the only means of transportation), safety of the observers, setting up of a field laboratory for analyses of the samples and because it fitted well with the ongoing project SEP 2014.

The present observations reported here were carried out during 2014 at the TSL Kaikhali, which had been one of the selected stations in SEP 2011. Moreover, this station was also chosen for the present time series observation, on the basis of our earlier sampling experience and a preliminary survey of the local fisherman community. The region around Kaikhali is highly productive and conducive to natural prawn larvae collection and is fully covered by mangrove forests on both sides of the river. The water quality of this study station is highly influenced by tidal variations as described in an earlier report (Nandy et al. 2018a).

The present observations were carried out over entire tidal cycles during Spring (9^{th} -12^{th} August 2014) and Neap (15^{th} -18^{th} August 2014) phases at the fixed station located at the confluence of Matla and Thakuran rivers in the Sundarbans Estuarine System (SES), India (Fig. 1). To understand the diel and tidal variability, zooplankton and water samples were collected between 03:00 a.m. to 03:00 a.m. of the next day at every 3 h interval, for 72 hours covering the entire tidal cycle of both spring and neap tidal phases. During the observation period, the times of sunrise and sunset were verified to be around 05:45 a.m. IST and 05:30 p.m. IST. Hence, the samples collected during 06 a.m. IST - 03 p.m. IST was considered as day time.

Samplings and Methods

The water level was measured hourly using the standard methodology used during SEP 2011. The mechanized boat with 4-6 cylinder engines and a standard tide gauge (Virtual Tide Staff or VTS) were used for water level measurement following standard protocol as described in SES 2013 at a fixed point. Moreover, to understand the water currents, a calibrated flow meter (Hydro Bios) was deployed at upper layer (30 cm depth from surface) in a position parallel to the river bank (Strydom and Wooldridge 2005). The water velocity ($m.s^{-1}$) was measured simultaneously from the rotor constant of the flow meter during both tidal phases.

Zooplankton samples were collected from the upper layer (at least 30 cm depth from surface), by 10 minutes horizontal tows with a round neck conical plankton net (mouth area 0.25 m^2 and mesh size 100μm) fitted with the calibrated flowmeter (Hydro Bios) at a fixed point (just beside the VTS) parallel to river bank. The flowmeter provided filtered volume measurements (in m^3) assuming 100% filtering efficiency. After collection, samples were immediately stored in plastic containers and preserved in 4% buffered formaldehyde solution (Harris et al. 2000). Different stages (mysis, decapodites and juveniles) of *M. dobsoni* were considered for this study because they were found the most abundant (>95%) in the collected samples and these stages are main target species for wild seed collectors. The larvae of *M. dobsoni* were further sorted with the help of a stereozoom microscope (Olympus SZ2-ILST) followed by identification. Different stages namely mysis, decapodites and juvenile were identified with the help of standard manual (Muthu et al. 1978) under the camera attached compound microscope (Nikon Eclipse E200). The qualitative and quantitative data was obtained from total filtered water of each collected plankton sample, and density was expressed as individuals per 100 m^3 of water (ind. 100 m^{-3}).

For water quality analysis, estuarine water (at 30 cm depth from surface) was collected using 5-liter Niskin-Water Samplers. Water temperature was recorded using mercury thermometer and the pH was measured using digital pH meter (Thermo-scientific, model: Orion Star-A311) in situ. Winkler titration method following Grasshoff et al. (1999) was used to measure dissolved oxygen (DO) concentration in the collected water sample. Samples for nutrient analysis were filtered through Whattman GF/F filter paper (mesh size-0.7 µm) and stored in 1-litre HDPE plastic bottles. Post collection, the samples were stored in multiple ice-boxes and transported to the laboratory for further analysis. Five major nutrient concentrations were analyzed using a spectrophotometer followed by standard protocol (Grasshoff et al. 1999), a relative error of accuracy was ±2.3% for phosphate; ±3.5% for nitrate and nitrite; ±6.6% for ammonia and ±5.6% for silicate. For chlorophyll *a* analysis, 1 L of the seawater was collected in dark bottles and filtered through a glass fibre filter (GF/F filter paper, mesh size-0.7 µm); pigments were extracted from the filter paper after incubation in 90% acetone and kept overnight at 4°C. The sample was then centrifuged at 5000 rpm for 10 min for collecting the supernatant and their concentration was estimated using a spectro-photometer (Shimadzu UV-1800) according to standard protocol (Strickland and Parsons 1972). All the environmental parameters were analyzed on the same day (except chlorophyll *a*) after bringing them to the laboratory.

Data Analysis

A two way Permutational Analysis of Variance (PERMANOVA) was applied to unravel the impact of tide and time on the abundance of different stages of *M. dobsoni*. Permutations of residuals under the full model with 999 numbers of permutations were used for the analysis. Both main test (using tide and time) and pair wise test (wherever significant, i.e. $p \leq 0.05$) were performed for each of the variables. The densities of three stages were considered as response variables, however times (day/night) and tides (high/low) considered as continuous variables. The water level below 3 m was considered as low tide condition for the analysis and it was performed for both tidal phases separately.

A Spearman Rank correlation matrix was also constructed to recognize the statistical relationship between different biotic and abiotic variables. The hypothesis test was performed to understand whether the correlation coefficient ρ is "close to zero" or "significantly different from zero". We decided this based on the sample correlation coefficient r and the sample size n, using a significance level of 5%, $\alpha = 0.05$. The tidal and diel variations of different larval stages and percentages of composition were plotted using Sigma-plot version 3.1 software; and different statistical analyses were done with the help of Excel-Stat and PRIMER version 6.0 (Clarke and Gorley 2006).

Results

Tides and Water Velocity

The area falls under a macro-tidal estuarine complex. There was significant variation in water levels measured between the two tidal phases. During the spring phase, the lowest low tide level was 0.80 m and the highest high tide level rose to 5.50 m. During the neap phase, the lowest low tide level was 1.12 m while the highest high water level was observed to be 4.88 m. The velocity of water was recorded and found to vary from 0.26 ms^{-1} to 4.17 ms^{-1} during the spring phase and from 0.12 ms^{-1} to 2.73 ms^{-1} to during the neap phase (Table 1; Fig. 2).

Physicochemical Parameters

The variations in physicochemical characteristics of water are presented in Fig. 3. The values observed during spring and neap phases are shown in Fig. 3a–j respectively. The maximum and minimum values of all the physicochemical parameters obtained during both tidal phases at day and night time are shown in Table 1. Correlation matrices were constructed in order to understand the role of the different hydrological parameters in structuring *M. dobsoni* abundance at the water column (Table 2a, b).

Total Abundances of *M. dobsoni*

Different stages of *M. dobsoni* were recorded and their total abundances varied according to diel and tidal scales during both spring and neap phases (Table 3). During spring phase, between high and low tide a significant variation in total abundance was also recorded (p=0.022; F=3.6993). Furthermore, comparatively higher abundance had been observed at low tide condition (water level<3 m) during the spring. The total night time abundance was observed to be

Table 1 Summary of different hydrological parameters during sampling periods

Parameters	Spring phase				Neap phase			
	Day Time		Night Time		Day Time		Night Time	
	Max	Min	Max	Min	Max	Min	Max	Min
Water level (m)	5.50	0.80	5.26	0.48	4.88	1.12	4.62	1.26
Current velocity ($m.s^{-1}$)	3.78	0.44	4.17	0.26	2.20	0.12	2.73	0.20
Water temperature (°C)	31.00	30.00	30.50	30.00	30.50	28.50	30.50	28.50
Dissolved Oxygen ($mg.L^{-1}$)	5.60	4.63	5.39	4.42	5.17	3.34	5.39	2.80
Salinity	23.83	19.59	23.72	16.54	22.32	16.24	22.17	11.44
pH	7.68	6.39	7.68	6.67	7.48	6.45	7.52	6.66
Chlorophyll-a ($\mu g.L^{-1}$)	3.68	0.78	2.20	0.13	3.86	0.67	3.53	0.17
Nitrite-N (µM)	9.20	1.26	14.98	1.15	3.56	0.96	3.72	0.84
Nitrate-N (µM)	31.76	12.75	26.12	13.31	41.08	12.71	41.95	21.75
Ammonium-N (µM)	1.70	0.26	1.74	0.18	1.68	0.02	3.01	0.04
Phosphate-P (µM)	5.65	0.96	1.47	0.92	0.11	0.02	0.15	0.03
Silicate (µM)	38.39	15.72	40.20	15.07	137.28	37.06	78.66	29.31
Total abundance (ind. 100^{-3})	418	2	300	2	132	3	419	18

comparatively higher than during the day time of the neap phase. Furthermore, during this phase the results obtained by using PERMANOVA clearly affirm a significant (p=0.008; F=7.6976) change between daytime and night time abundances. In addition to this, during high tide conditions, the total abundance was found to fluctuate significantly (p=0.01) between daytime and night time values.

Diel and Tidal Influence on Abundance of Different Stages of *M. dobsoni*

During the spring phase, maximum numbers of juveniles were found in comparison to other stages in the low tide periods, with values ranging from 2 ind.100 m^{-3} to 414 ind.100 m^{-3} at day and from 9 ind.100 m^{-3} to 264 ind.100 m^{-3}at night. Moreover, the tide (p=0.04; F=3.834) and time (p=0.017; F=5.6709) play a significant role in their density variation during this phase. Howbeit, the maximum variation in abundance was recorded during day time between high and low tide (p=0.001). Additionally, mysis was recorded as the second most dominant stage (Table 3; Fig. 4a) ranging from 3 ind. 100m^{-3} to 65 ind. 100 m^{-3} during day and 2 ind. 100 m^{-3} to 99 ind. 100m^{-3} at night . PERMANOVA results also confirm a significant variation in their abundance with the tidal (p=0.01; F=2.4706) and temporal (p=0.007; F=2.7246) variations.

However, during the neap phase the mysis stage occurred predominantly at low tide conditions, whereas the next dominant juvenile stages were recorded only at night time irrespective of high or low tide conditions (Fig. 4b). The density of the mysis stage changed significantly with tide (p=0.032; F=4.2587) and also during day time (p=0.043), between high and low tides. Likewise, the abundance of juvenile varied significantly with time (p=0.001; F=13.298) and especially during high tide conditions (p=0.001, between day and night). The maximum night catches of mysis and juveniles were recorded respectively as 368 ind.100 m^{-3} and 340 ind.100 m^{-3} and the minimum values were found to be 9 ind.100 m^{-3} and 4 ind.100 m^{-3} respectively (Table 3). The decapodite stages recorded the lowest numbers during both tidal phases. Their maximum abundances were observed to be higher during the night (38 ind.100 m^{-3} and 51 ind.100 m^{-3} during spring and neap respectively) than during the day (5 ind.100 m^{-3} and 4 ind.100 m^{-3} during spring and neap respectively).

The overall percentages of different stages were also observed and it showed a significant variation between the two tidal phases (Fig. 5).

Discussion

The present observation was carried out during a peak monsoon season (August 2014). By this time, a major part of the SES was altered into low salinity and brackish water zones due to the huge monsoonal precipitation and associated river runoff. According to Nandy and Mandal (2020), during Indian summer monsoon which is a cyclic event, a change in estuarine water quality occurs. Earlier studies (Attri and Tyagi 2010; Chowdhury et al. 2012; Nandy et al. 2018b) reported that nearly 70% of the annual rainfall, typically around 1500 – 2500 mm occurs during this summer monsoon period. The impact of the monsoonal rainfall was clearly evident in our study, as the lowest salinity was found to be 11.44 during the sampling period. The water temperatures varied due to the availability of sunlight and,

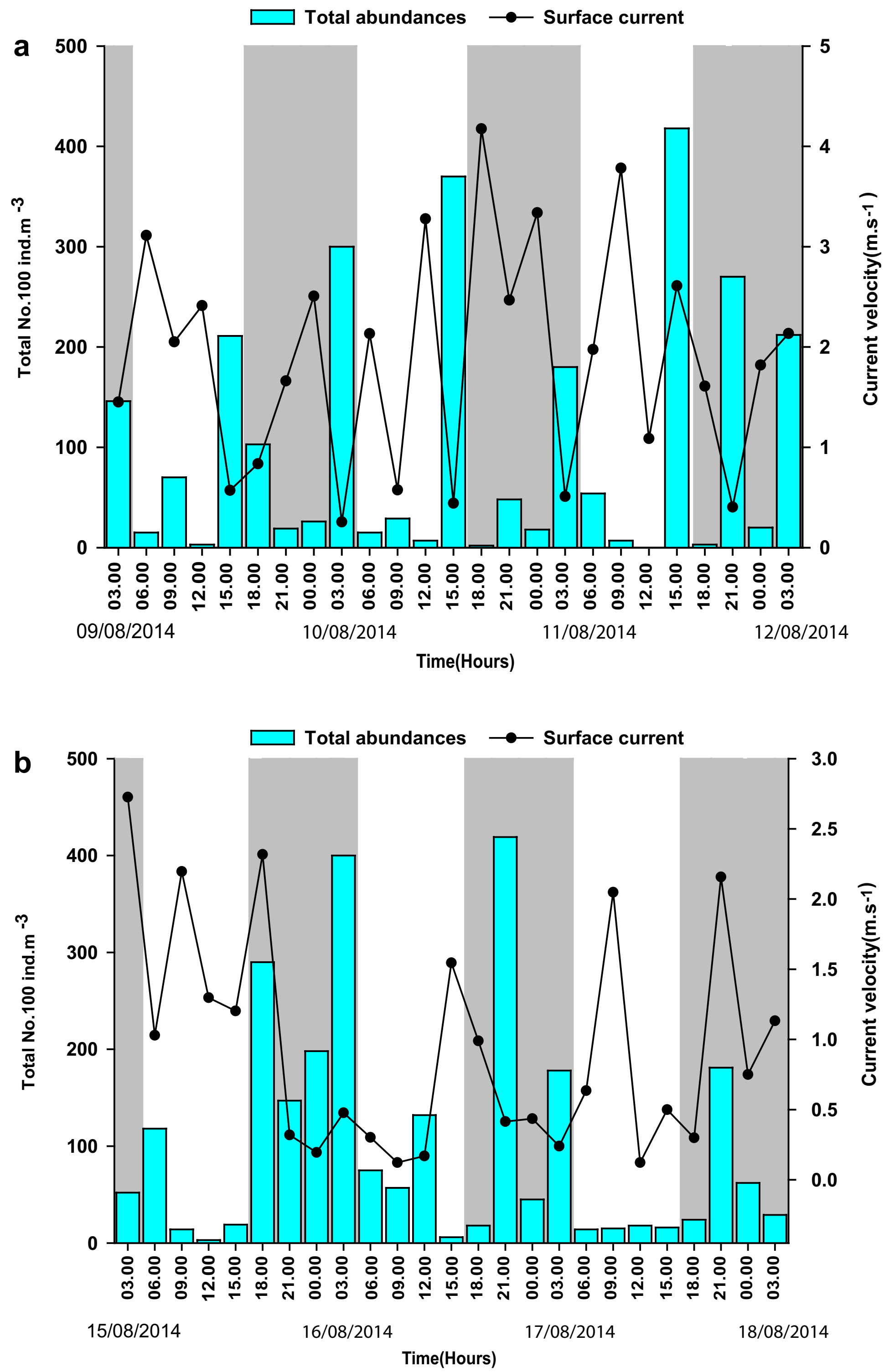

Fig. 2 Diel changes of total populations associated with surface water currents during, (**a**) spring tide and (**b**) neap tide

for that reason minimum temperatures were recorded only at night during both tidal phases.

The concentration of DO was found to be positively correlated with salinity and the tidal water level, indicating the presence of a more oxygenated water mass during the high tide of spring phase. Remarkable diel and tidal variations of the various nutrient concentrations were recorded during both tidal phases, which might be due to the effect of different biogeochemical activity within the estuary (Nandy et al. 2018a). The total shrimp abundances, as well as the different stages, were not significantly affected by any water quality characteristics of the estuary.

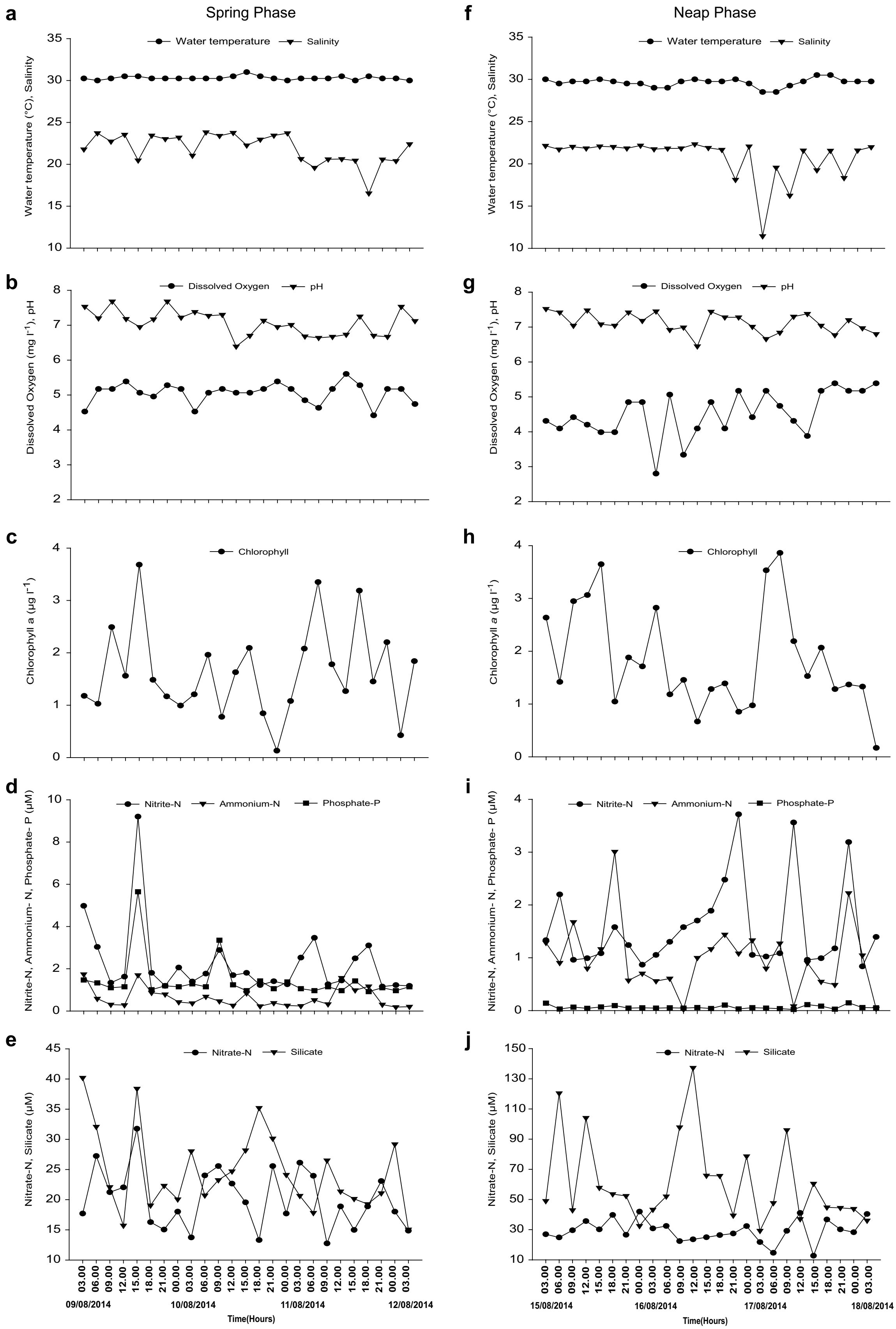

Fig. 3 Variation in different water quality parameters during (**a**-**e**) spring and (**f**-**j**) neap tide

Table 2 Correlations matrices of different hydrological parameters with total abundances, during (**a**) spring and (**b**) neap tide. Bold values are significant

A. Spring tide

Hydrological parameters	Water level(m)	Current Velocity (m.s^{-1})	Water temperature(°C)	DO (mg. L^{-1})	Salinity(psu)	pH	Chlorophyll-*a* (µg.L^{-1})	Nitrite-N (µM)	Nitrate-N (µM)	Ammonium-N (µM)	Phosphate-P (µM)	Silicate (µM)	Total Larval abundance (Ind.m^{-3})
Water level(m)	1.000												
Current Velocity(m. s^{-1})	0.235	1.000											
Water temperature(°C)	−0.220	−0.264	1.000										
DO (mg.L^{-1})	**0.703**	0.271	0.043	1.000									
Salinity(psu)	0.391	0.305	−0.141	**0.453**	1.000								
pH	0.123	−0.026	−0.374	0.054	0.325	1.000							
Chlorophyll(µg.L^{-1})	-0.430	−0.211	0.078	−0.180	−0.366	−0.265	1.000						
Nitrite-N(µM)	**−0.476**	−0.287	0.124	−0.279	−0.281	−0.049	**0.488**	1.000					
Nitrate-N(µM)	0.012	−0.281	0.105	0.108	0.067	−0.246	0.264	**0.550**	1.000				
Ammonium-N(µM)	−0.359	−0.362	0.260	−0.126	−0.339	0.023	0.274	**0.664**	0.129	1.000			
Phosphate-P(µM)	−0.139	−0.258	0.089	0.043	−0.017	0.052	0.339	**0.807**	**0.504**	0.394	1.000		
Silicate(µM)	−0.144	0.064	0.178	−0.050	0.058	0.158	−0.172	**0.489**	0.140	0.351	0.438	1.000	
Total abundance(Ind. m^{-3})	**−0.476**	**−0.492**	0.062	−0.229	−0.236	−0.039	**0.495**	0.174	−0.080	0.175	0.130	0.051	1.000

B. Neap tide

Hydrological parameters	Water level(m)	Current Velocity(m. s^{-1})	Water temperature(°C)	DO(mg. L^{-1})	Salinity(psu)	pH	Chloro-phyll-*a* (µg.L^{-1})	Nitrite-N (µM)	Nitrate-N (µM)	Ammonium-N (µM)	Phosphate-P (µM)	Silicate(µM)	Total Larval abundance (Ind.m^{-3})
Water level(m)	1.000												
Current Velocity(m. s^{-1})	−0.151	1.000											
Water temperature(°C)	0.067	0.144	1.000										
DO (mg.L^{-1})	−0.001	−0.088	0.112	1.000									
Salinity(psu)	0.071	0.114	0.428	−0.326	1.000								
pH	−0.111	0.319	0.071	−0.329	0.201	1.000							
Chlorophyll(µg.L^{-1})	0.211	0.164	−0.415	−0.221	−0.323	0.135	1.000						
Nitrite-N(µM)	**−0.574**	0.138	0.079	0.076	−0.338	0.233	−0.325	1.000					
Nitrate-N(µM)	0.104	0.143	0.146	−0.042	0.354	0.142	−0.345	−0.105	1.000				
Ammonium-N(µM)	−0.243	**0.512**	0.064	−0.039	0.088	0.055	0.010	0.109	0.096	1.000			
Phosphate-P(µM)	0.023	0.440	0.274	−0.079	0.114	0.196	−0.036	0.014	0.100	**0.549**	1.000		
Silicate(µM)	−0.061	−0.069	0.140	−0.402	0.198	-0.017	−0.156	0.224	−0.254	−0.147	−0.258	1.000	
Total abundance(Ind. m^{-3})	−0.187	−0.058	−0.172	−0.157	−0.186	0.109	−0.134	0.286	0.124	0.228	−0.044	−0.223	1.000

Table 3 Variations of different stages of larval and juveniles density (ind.100 m^{-3}) during sampling periods

	Spring Tide				Neap Tide			
	Day		Night		Day		Night	
	Max	Min	Max	Min	Max	Min	Max	Min
Mysis	65	3	99	2	132	3	368	9
Decapodite	5	2	38	3	4	0	51	6
Juvenile	414	2	264	9	57	7	340	4

Similar to other penaeid prawns, *M. dobsoni* has been known to spend a part of their life cycle in estuarine waters. As the present study was conducted during August, we did not observe the eggs and early larval stages such as nauplii or protozoea in the samples which was most probably due to the fact that most of them had already matured to the mysis stage before coming to this estuarine area. This is in accordance to the studies of Menon (1952) and George

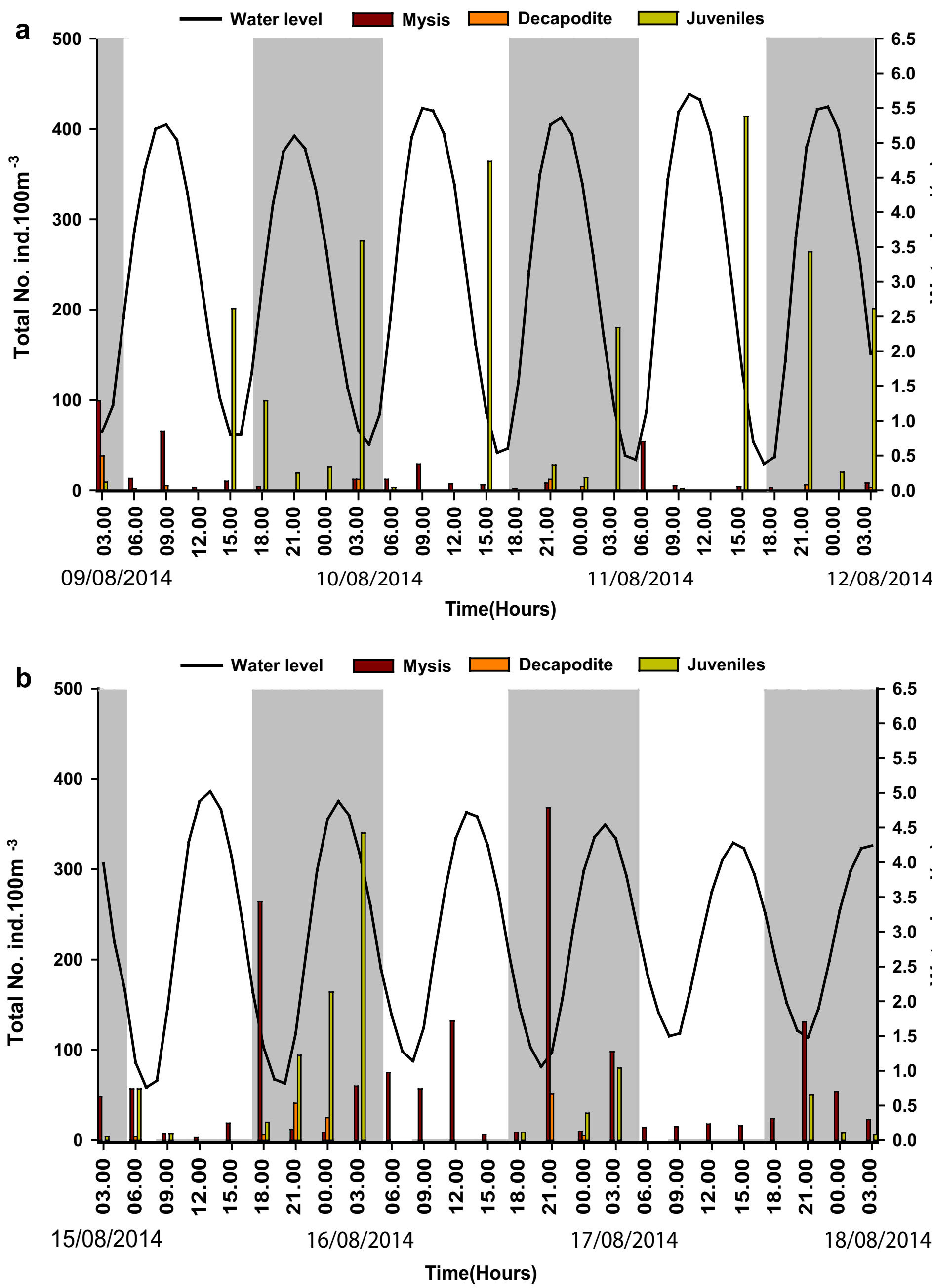

Fig. 4 Diel and tidal changes of different stages of *M. dobsoni*, during (**a**) spring and (**b**) neap tide. Shaded portions indicated the night time of the sampling period and black line indicated the water level

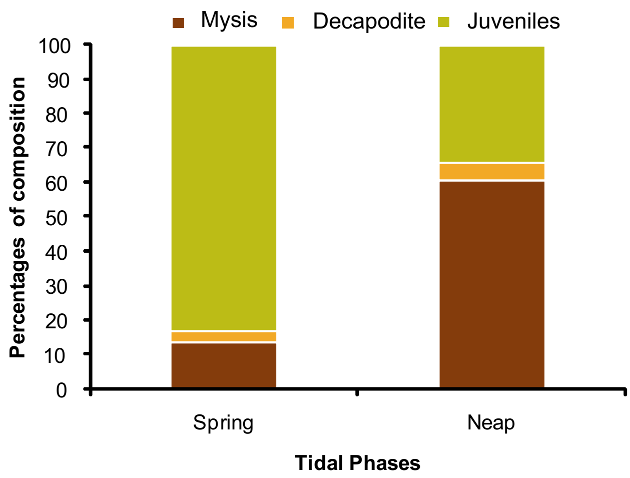

Fig. 5 Percentages of composition of different stages of *M. dobsoni*, during spring and neap tide

(1962) who had found that eggs and larva occur near the Cochin brackish waters between September and April. The eggs are released in the in-shore coastal waters or in the sea at 25m depth zone and mysis ingresses into the estuarine system for further development until they reach the juvenile stage (Menon 1952, 1955; Sukumaran et al. 1993).

The turbidity of the waters in the SES estuaries is very high due to the high sediment load; the turbid water mass comes from the northern parts of India carrying with it sediments of Himalayan origin and associated land and river runoff during rainy season (Nandy et al. 2018b). The water carries a huge amount of suspended particulate matter during this time in the SES. Moreover for the meroplankton community, the vertical tidal migration is also advantageous as it helps to avoid visually oriented predators like carnivorous fish and other aquatic organisms (Bollens and Frost 1991) and also protects them with low water transparency (Williamson et al. 2011). Due to this phenomenon, during the neap phase of our study, the maximum abundance of total population (dominated by mysis stages) was observed at night time. The spring tide samples did not exhibit such mechanisms due the dominance of larger juvenile stages during this time.

The highest record of juveniles observed during the spring ebb tides, indicates the probable egress of the juvenile stages using the ebb tidal currents as the tidal amplitude during this period is higher (0.48 m to 5.50 m) than during the neap phase. However, the abundance of the mysis stage is highest during the neap phase. From the recorded observations it can be assumed that, as the mysis stages are not very good swimmers, they probably use vertical migration during low tidal amplitudes (1.12 m to 4.88 m) of the neap tide to remain in the estuarine system. These larvae have to rely on tidal currents for ingress and retention into the estuarine system until further development. This behavioural pattern of the stages could be ecologically advantageous to them as it would prevent them from getting washed out from their preferred ecological habitat (Morgan 1995).

In the present study, we recorded a significant ($p \leq 0.05$) diel and tidal variation in abundance of different stages of *M. dobsoni* for the first time. Their selective preference of tide and time might be a migration pattern and/or predator avoidance mechanism. Either the majority of juvenile population might be egressed out during spring phase or they might be shifted towards another habitat (benthic), which would be a possible reason for lower abundance recorded during the neap phase. Moreover, lower abundance of decapodites throughout the study may imply their avoidance of the central parts of the estuary in order to remain in their preferred habitat (river bank or tidal inlet). We have also noticed from our personal observations, local larvae collectors prefer river banks and small shallow tidal creeks for collecting this stage. Furthermore, the decapodites stage is very short lived (6-7 days) and their mortality rate is very high (more than 90%) which might be another plausible reason for their lowest abundance observed in the present study (Treece and Yates 1988).

In general, the current speeds are higher during flood and ebb phase (Wooldridge and Erasmus 1980; Ueda et al. 2010) and decrease with channel depth due to bottom friction (Hill 1991). The important feature observed during the present study was, the coincidence of the peak larval accumulation in the water during minimum current speeds. This is consistent with the observations in different estuaries worldwide, where the zooplankton migrates with the tides and currents to escape from getting flushed out from the estuaries (Laprise and Dodson 1989; Ueda et al. 2010; Vineetha et al. 2015). As the SES is known to be the best nursery ground for different shellfish communities, this behavioural pattern of *M. dobsoni* can be explained by the position-dependent vertical migration in their suitable estuarine habitat.

The rivers in Sundarbans have shallow depths (3-10m) and are macrotidal. Accordingly, the huge tidal variations perhaps influence the migration patterns of penaeid larval stages along with diel variations. Moreover, it has been significantly ($p \leq 0.05$) established that the neap phase flood tides are the best times for the larva (mainly mysis stages) collection in this estuary and spring tide is very much suitable for decapodites and juvenile catches.

Proper control and supervision should be maintained during wild seed collection at the spring phase, as it is dominated by matured forms (mainly juveniles) that migrate to their native habitat towards the open sea for further development. The present study provides detailed information about the most productive wild seed collection time, which in turn can help the fishermen to reduce their effort of fishing and wastage of non-target meroplankton species. This is very essential for rural socio-economy as well as sustainable fishery development in Indian Sundarban.

Conclusion

The present study is a maiden effort to assess the diel and tidal variations on the abundance of penaeid shrimp larvae in a single layer, using *M. dobsoni* as a proxy, at SES. The outcome of our study noticeably indicated a significant abundance of different stages of *M. dobsoni.* Current velocity plays a fundamental role in the abundance of larvae in the water column.

The present study would help fishermen to identify the suitable time to collect *M. dobsoni* larvae from SES by identifying the periods during which prawn catch can be optimized. The overall abundances are comparatively higher at night time and the low tide during spring tidal phase is used by the decapodites and juveniles to retreat to the open coastal waters. Moreover, the mysis stages probably prefer flood tide to ingress into the estuarine brackish water during neap phase. Total abundances are observed to be significantly high during selective tidal phases, and low water currents. These unique combinations of the physical conditions indicate their behavioural pattern for retaining their position in the suitable estuarine habitat of the SES. So, the present findings will be helpful for understanding the adaptive strategies adopted by *M. dobsoni* for their larval retention in the estuaries which could give an insight into the stock population. Future studies on other commercially important penaeid prawn larval migration would be advantageous in terms of population dynamics and sustainable management of those species in SES.

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Declarations

Ethical Approval This article does not contain any studies with animals performed by any of the authors.

Conflict of Interest The authors declare that they have no conflict of interest.

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