

## Seasonal dynamics of fish assemblages in an intertidal mudflat of Indian Sundarbans

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**SUMMARY:** In the present study, the seasonal and inter-annual fish assemblage structure of intertidal mudflats of Indian Sundarbans was analysed during tidal cycles. A total of 31 fish species belonging to 22 families and 9 orders were collected during high tide, whereas only 12 were recorded during low tide. Fish assemblage descriptions were based on several community descriptors, namely diversity ( $H'$ ), species richness (S), species dominance (D), and species evenness (J) and on an ecological guild classification. A canonical correspondence analysis (CCA) was performed to evaluate the relationship between estuarine habitat and fish assemblages in the mudflat habitat during inundated and exposed conditions. All the diversity indices showed marked seasonal and inter-annual variations. Temporal variations were also found in fish assemblage structure in both tidal conditions. Estuarine species were the most important ecological guild of the mudflats during both high and low tides. Of all the abiotic variables examined, CCA showed that salinity, pH and nutrients were the most important influencing fish assemblage during high tide. Total dissolved solids, water temperature and salinity were significant during low tide. Considering the importance of mudflats in supporting fish diversity, the present study emphasizes the increased efforts for conservation of this habitat in the Indian Sundarbans.

**Keywords:** ichthyofaunal diversity, seasonal variation, tidal variation, mudflats, Bray-Curtis similarity, CCA.

**RESUMEN:** DINÁMICA ESTACIONAL DE COMUNIDADES DE PECES EN UNA MARISMA INTERMAREAL DE SUNDARBANS INDIO. – En el presente estudio, la estructura estacional e interanual de comunidades de peces en el intermareal fangoso de Sundarbans se analizó durante ciclos de marea. 31 especies pertenecientes a 22 familias y 9 órdenes fueron recogidas durante la marea alta, mientras que sólo 12 se registraron durante la marea baja. Las comunidades se describieron varios descriptores: diversidad ( $H'$ ), riqueza de especies (S), dominancia de especies (D) y uniformidad de especies (J) y una clasificación ecológica de comunidad. Se realizó un análisis de correspondencia canónico (CCA) para evaluar la relación entre hábitat estuárico y comunidades de peces durante condiciones inundadas y expuestas. Todos los índices de diversidad mostraron marcadas diferencias estacionales e interanuales. También se encontraron variaciones temporales en la estructura del conjunto de peces en tanto las condiciones de la marea. Especies estuarinas (ES) fue el grupo ecológico más importante de las marismas de Sundarbans tanto durante la marea alta como en la baja.

**Palabras clave:** diversidad íctica, variación estacional, variación de marea, marismas, similitud de Bray-Curtis, CCA.

### INTRODUCTION

Estuaries and coastal lagoons show high levels of habitat heterogeneity and support a large fish production (Elliott and Hemingway 2002). Estuarine fish assemblages change significantly in relation to habitat characteristics and in particular to the degree of habitat complexity (Sogard and Able 1991, Connolly 1994, West and King 1996, Jenkins and Wheatley 1998, Paterson and Whitfield 2000).

Mudflats are a dominant habitat in many estuaries, often covering a considerable part of the total estuarine area. This particular type of habitat has been recognized to be of key importance for the estuarine food web due to its high productivity when compared with subtidal areas (Elliott and Dewailly 1995). Mudflats are structurally less complex than mangroves, but they contain great abundance and diversity of invertebrates and are periodically immersed and emerged in each tidal cycle. They are therefore only available to nekton during tidal

inundation, which implies tidal migrations to use this habitat (Nagelkerken and van der Velde 2002, Pihl and Wennhage 2002, Weerts and Cyrus 2002, Mumby *et al.* 2004, Castillo-Rivera *et al.* 2010). However, unlike estuarine salt marshes, which have long been considered highly productive habitats and have been thoroughly studied (Cattrijsse *et al.* 1997, Halpin 2000, Hampel *et al.* 2003), mudflats have only recently become an object of study (Morrison *et al.* 2002, Melville and Connolly 2005, Dolbeth *et al.* 2007, Nip and Wong 2010).

Besides the differences in fish assemblages associated with the various habitat types, ichthyofaunal compositions and structure can also undergo consistent cyclical and temporal changes within habitats. Seasonal shifts in fish communities are common, as a result of sequential immigration and emigration of certain fish species (Hyndes *et al.* 1999, Thiel and Potter 2001). Tidal shifts in fish assemblages have also been reported by several authors (Sogard *et al.* 1989, Rountree and Able 1993, Gray *et al.* 1998, Griffiths 2001, Methven *et al.* 2001, Morrison *et al.* 2002, Guest *et al.* 2003). Several environmental factors, in addition to habitat availability, contribute to fish assemblage structure in different spatial and temporal scales (Thiel *et al.* 1995, Methven *et al.* 2001).

The Sunderbans mudflats (Banerjee 1998, Bose 2004) are found at the estuary and on the deltaic islands where velocity of river and tidal current is low. The flats are exposed at low tides and submerged at high tides, thus being changed morphologically even in one tidal cycle. The interior parts of the mudflats are a magnificent home of luxuriant mangroves. The Sunderbans mudflats control the food chain in the estuarine ecosystem.

This study aims (1) to characterize the nekton assemblage of the mudflat habitats of the Sunderbans estuary, (2) to assess the effect of seasonal and inter-annual variations in fish assemblage structure in two tidal phases, and (3) to relate environmental variables with fish assemblages. These should provide a better understanding of the role of the strait in supporting coastal fish communities.

## MATERIALS AND METHODS

### Study area

The total area of the Sundarban region in India is 9630 km<sup>2</sup>, which constitutes the Sundarban Biosphere Reserve between 21°40'04"N and 22°09'21"N and between 88°01'56"E and 89°06'01"E. The landscape is characterized by a web of tidal water systems. The mean depth of the estuary is 5 m and the maximum depth is 40 m near the mouth of the estuary. The river flow varies both seasonally and inter-annually, with a mean discharge of 400 m<sup>3</sup> s<sup>-1</sup> (Bettencourt and Ramos, 2003).

Twelve study sites with similar physical features (composed predominantly of well-packed soft mud) were selected randomly along a 10 km stretch of the

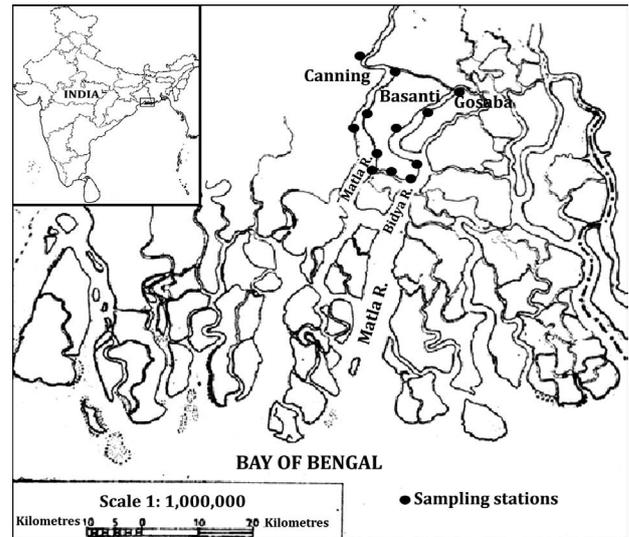


Fig. 1. – Map of the Indian Sundarbans showing the locations of study sites and sampling stations.

River Matla, the River Bidya, the Boro Hero bhangra rivulet and their adjacent mudflats in the Indian Sundarban (22°01'N, 88°40'E) (Fig. 1). The sampling covered a total area of 35 km<sup>2</sup> with a mean depth of 2.15±0.76 m and a tidal range of 3 m per 6 h.

### Sampling and environmental data

Sampling was conducted seasonally (pre-monsoon: February-May, monsoon: June-September and post monsoon: October-January) between October 2008 and September 2011. Fish sampling was performed during high tide with a gill net of 20 m length, with 1 cm spacing between adjacent knots. The nets were placed at the onset of high tide and kept for approximately 6 h in order to ensure maximum fish catch per unit effort during high tide. Sixteen nettings were undertaken at each site of this estuary per season, i.e. four nettings per month at each site. Four nettings were pooled together and represented here as single abundance data for each site per month. The replicate sites were sampled simultaneously and for the same tenure to minimize the sampling errors (single abundance data from each site, i.e. 12 replicates per month, 48 replicates per season and 144 replicates per year). During low tide a few 100 m transects were established at each study site to study the amphibious fishes. Along the transect 2×2 m quadrates constructed from nylon ropes and bamboo sticks were temporarily established at intervals of 8 m (approx. 10 quadrates per transect). Hand nets (dot net) were also used for sampling tidal pools during low tide. The specimens were retrieved from the net and identified, and species abundance was recorded to investigate species assemblages. Individuals representing each fish species were preserved in 5% formalin and the live fishes were measured for total length ( $L_T$ , cm) and released. Fish specimens were identified to the lowest taxonomic level following the existing literature

(Shaw and Shebbeare 1937, Day 1958, Talwar and Jhingran 1991).

At each sampling station, prior to netting hydrological parameters (water temperature, pH, total dissolved solids, salinity, inorganic phosphate, nitrate nitrogen, nitrite nitrogen and reactive silicate) were recorded during high tide following Strickland and Parsons (1972), Grasshoff *et al.* (1983) and Grasshoff (1983) and soil parameters (soil moisture, soil pH, soil organic matter and soil organic carbon) were recorded during low tide following Brower *et al.* (1998).

## Data analyses

Total fish abundance (number of individuals) was calculated for each season in each year. Species richness (S) (Margalef 1957), Pielou evenness (J) (Pielou 1969), species dominance (D) (Berger and Parker 1970) and the Shannon-Wiener diversity index (H') (Shannon and Wiener 1949) were calculated for high-tide and low-tide conditions in three seasons in each year. Cluster analysis with the Bray-Curtis similarity measure was used to determine similarity between seasonal nekton assemblages for each year during high tide and low tide on the basis of species abundance data using PRIMER 5 software. Results were displayed using non-metric multidimensional scaling plots, on which percentage similarity levels were assigned based on group-average linkage (Horinouchi 2009). The abundance data were square-root transformed when necessary. To determine whether or not major shifts in community structure had occurred between groups of seasons and between years, a non-parametric, permutation-based two-way analysis of similarity (ANOSIM, Clarke, 1993) was performed. Where appropriate, R-statistic values for pair-wise comparisons provide by ANOSIM was used to determine the dissimilarity between groups. Values close to 1 indicate very different composition, while values near zero show little difference. ANOSIM was used to test the null hypothesis that within seasons no changes in community structure were observed between years, and secondly to check that within years no changes in community struc-

ture were observed between seasons separately for high-tide and low-tide conditions. Species were classified by functional groups according to Franco *et al.* (2008) and each species was assigned to an ecological guild. The ecological guilds contained estuarine species (ES), marine migrants (MM), freshwater species (F), anadromous species (A) and catadromous species (C). Ecological guilds were analysed by both number of species and number of individuals within each guild. The percentage contribution of each functional category to the total species richness and species abundance was calculated for two tidal conditions in each season and in each year, and compared to assess the prevailing function of each system during the time period of the present study. Analysis of variance (ANOVA) was performed on hydrological parameters, diversity indices and ecological guilds. As the study focused mostly on the temporal factors (seasons and years) in two tidal phases, one-way ANOVA (Zar 1999) was carried out separately with seasons (three levels: pre-monsoon, monsoon and post monsoon) and years (year 1, year 2 and year 3) as factors. A Duncan test was used for post hoc comparisons after ANOVA. Statistical analyses were carried out by means of SPSS (Statistical Package for Social Sciences, version 17.0 Norušis 2000). Finally canonical correspondence analysis (CCA) (Ter Braak 1988; McGarigal *et al.* 2000) was performed in order to elucidate the possible relationships between biological assemblages of species and the hydrological variables during two tidal phases. The seasonal samplings from all the study sites in three years were included in the analysis. Rare species in the fish species matrix were downweighted following the CANOCO procedure in order to prevent them from having an excessive influence on the ordination. This analysis was carried out using CANOCO (ver. 4.5) software.

## RESULTS

Seasonal trends of water and soil parameters in three respective years are given in Table 1. All the parameters except soil organic carbon and soil organic matter varied significantly ( $p < 0.01$ ) between seasons

TABLE 1. – Water and soil parameters (abbreviations are in parenthesis) of studied mudflats of the Indian Sundarbans. Sal, salinity (PSU); W tm, water temperature (°C); TDS, total dissolved solids (g/L); I Phs, inorganic phosphate (µM/L); Na N, nitrate-N (µM/L); Ni N, nitrite-N (µM/L); Sil, reactive silicate (µM/L); S OC, soil organic carbon (%); S OM, soil organic matter (%); S Mo, soil moisture (%); S pH, soil pH.

Hydrological parameters	Pre-monsoon			Monsoon			Post-monsoon		
	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
Sal	26.74 <sup>a</sup> ±0.06	31.03 <sup>b</sup> ±0.56	31.05 <sup>b</sup> ±0.20	17.17 <sup>d</sup> ±0.33	16.79 <sup>d</sup> ±0.30	10.85 <sup>f</sup> ±0.29	24.86 <sup>e</sup> ±0.33	19.91 <sup>h</sup> ±0.56	17.32 <sup>±</sup> 0.43
W tm	31.56 <sup>a</sup> ±0.11	34.81 <sup>b</sup> ±0.26	34.21 <sup>b</sup> ±0.37	30.36 <sup>d</sup> ±0.28	29.62 <sup>e</sup> ±0.18	28.65 <sup>f</sup> ±0.22	24.81 <sup>g</sup> ±0.4	27.79 <sup>h</sup> ±0.16	24.41 <sup>±</sup> 0.53
pH	7.98 <sup>a</sup> ±0.07	7.14 <sup>b</sup> ±0.02	7.08 <sup>b</sup> ±0.02	7.86 <sup>a</sup> ±0.02	6.83 <sup>d</sup> ±0.02	7.06 <sup>b</sup> ±0.04	7.00 <sup>b</sup> ±0.02	6.99 <sup>b</sup> ±0.02	6.85 <sup>±</sup> 0.03
TDS	2.53 <sup>c</sup> ±0.07	3.16 <sup>a</sup> ±0.02	1.47 <sup>b</sup> ±0.06	2.40 <sup>±</sup> 0.05	1.31 <sup>d</sup> ±0.03	1.96 <sup>b</sup> ±0.08	1.35 <sup>b</sup> ±0.04	0.72 <sup>±</sup> 0.12	1.24 <sup>b</sup> ±0.13
I Phs	0.14 <sup>a</sup> ±0.03	0.79 <sup>b</sup> ±0.16	1.17 <sup>c</sup> ±0.02	1.56 <sup>d</sup> ±0.12	2.11 <sup>e</sup> ±0.51	2.57 <sup>f</sup> ±0.94	1.04 <sup>±</sup> 0.01	2.36 <sup>e</sup> ±0.03	2.15 <sup>h</sup> ±0.19
Na N	0.95 <sup>a</sup> ±0.14	2.84 <sup>b</sup> ±0.08	2.24 <sup>c</sup> ±0.68	2.06 <sup>d</sup> ±0.05	3.13 <sup>e</sup> ±0.11	6.27 <sup>f</sup> ±0.11	2.30 <sup>±</sup> 0.0	3.44 <sup>h</sup> ±0.05	6.98 <sup>±</sup> 0.05
Ni N	0.31 <sup>a</sup> ±0.03	0.69 <sup>b</sup> ±0.01	1.09 <sup>c</sup> ±0.06	0.35 <sup>a</sup> ±0.02	0.73 <sup>b</sup> ±0.06	1.50 <sup>d</sup> ±0.05	0.57 <sup>±</sup> 0.06	0.79 <sup>b</sup> ±0.02	2.26 <sup>±</sup> 0
Sil	8.05 <sup>a</sup> ±0.10	7.90 <sup>a</sup> ±0.09	12.95 <sup>b</sup> ±2.15	16.70 <sup>d</sup> ±0.47	17.80 <sup>d</sup> ±0.51	17.97 <sup>d</sup> ±0.93	7.76 <sup>a</sup> ±0.04	7.71 <sup>a</sup> ±0.04	18.08 <sup>h</sup> ±0.07
S OC	0.91 <sup>a</sup> ±0.04	0.91 <sup>a</sup> ±0.04	0.91 <sup>a</sup> ±0.04	0.98 <sup>a</sup> ±0.01	0.98 <sup>a</sup> ±0.01	0.98 <sup>a</sup> ±0.01	0.90 <sup>a</sup> ±0.03	0.90 <sup>a</sup> ±0.03	0.90 <sup>a</sup> ±0.03
S OM	1.57 <sup>a</sup> ±0.06	1.55 <sup>a</sup> ±0.06	1.56 <sup>a</sup> ±0.06	1.69 <sup>a</sup> ±0.01	1.69 <sup>a</sup> ±0.01	1.69 <sup>a</sup> ±0.01	1.55 <sup>a</sup> ±0.05	1.55 <sup>a</sup> ±0.05	1.55 <sup>a</sup> ±0.05
S Mo	54.81 <sup>a</sup> ±2.06	54.8 <sup>a</sup> ±2.06	55.70 <sup>a</sup> ±2.06	55.70 <sup>a</sup> ±1.22	55.70 <sup>a</sup> ±1.22	55.70 <sup>a</sup> ±1.22	44.79 <sup>e</sup> ±1.17	44.79 <sup>e</sup> ±1.17	44.79 <sup>e</sup> ±1.17
S pH	7.40 <sup>a</sup> ±0.06	7.40 <sup>a</sup> ±0.06	7.40 <sup>a</sup> ±0.06	7.13 <sup>d</sup> ±0.04	7.13 <sup>d</sup> ±0.04	7.13 <sup>d</sup> ±0.04	7.71 <sup>±</sup> 0.02	7.71 <sup>±</sup> 0.02	7.71 <sup>±</sup> 0.02

N.B.: Different letters indicate significant differences at 0.05% level of significance.

TABLE 2. – Percentage abundance of the species (units and abbreviations are in parenthesis) caught in each season in mudflat habitat during high tide and low tide in three different seasons in three respective years (Y1, Y2, Y3). The ecological guilds (EG) are indicated for each species: ES, estuarine species; MM, marine migrant; C, catadromous; A, anadromous; F, fresh water species).

Family	High tide			High tide			High tide			Low tide			Low tide			EG			
	Pre-monsoon			Monsoon			Post-monsoon			Pre-monsoon			Monsoon				Post-monsoon		
	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3	Y1	Y2	Y3		Y1	Y2	Y3
<i>Boleophthalmus boddarti</i> (Bo.bo)	4.2	0	0	0.7	0	0	1.2	0.4	0	6.3	6.4	7.0	13.8	13.3	13.6	30.6	20.4	10	ES
<i>Bregmaceros maclellandi</i> (Br.mc)	1.2	0	18.9	0	8.5	23.4	0	11.5	47.7	0	0	0	0	0	0	0	0	0	MM
<i>Butis butis</i> (Bu.bu)	0	0	0	0	0	0	0	0.7	0.4	0	0	0	0	0	0	0	0	0	ES
<i>Coilia neglecta</i> (Co.ne)	0	0	0	37.5	17.9	1.4	15.3	0	1.4	0	0	0	0	0	0	0	0	0	ES
<i>Coilia ramcarati</i> (Co.ra)	24.2	6.5	36.9	12.5	29.2	37.4	17.9	1.8	16.2	0	0	0	0	0	0	0	0	0	ES
<i>Cynoglossus lingua</i> (Cy.li)	0	8.8	0	0.3	1.2	0.1	0.2	2.6	0	0	0	0	0	0	0	0	0	0	ES
<i>Glossogobius giuris</i> (Gl.gi)	1.2	0	0	0	0.9	0	0.2	0.3	0	0	0	0	0	0	0	0	0	0	C
<i>Gudusia chapra</i> (Gu.ch)	26.7	7.7	17.2	16.9	2.1	0.9	19.0	3.2	1.1	0	0	0	0	0	0	0	0	0	F
<i>Himantura walga</i> (Hi.wa)	2.4	0	0	2.0	0.4	0.2	5.6	0.6	0.1	0	0	0	0	0	0	0	0	0	MM
<i>Hyporhamphus limbatus</i> (Hy.li)	0	0	0	0	0.5	0	1.9	0	0	0	0	0	0	0	0	0	0	0	F
<i>Liza parsia</i> (Li.pa)	22.4	18.2	11.1	11.5	7.0	2.6	9.0	15.1	1.4	0	0	0	0	0	0	0	0	0	C
<i>Moringua raitabarua</i> (Mo.ra)	1.2	5.4	0	0.3	0	0.1	0	0	0	6.9	0	0	2.2	1.0	0	0.4	0	0	ES
<i>Muraenesox bagio</i> (Mu.ba)	0	0.5	0.3	0.3	1.0	2.3	2.8	6.0	0.4	0	0	0	5.8	0	0	0.7	0	0	MM
<i>Mystus gutto</i> (My.gu)	1.8	12.4	9.4	2.7	2.2	0	0	0	0	0	0	0	0	0	0	0	0	0	A
<i>Ophichthus apicalis</i> (Op.ap)	1.8	1.4	0.3	0	0	0	0	0	0	2.1	0	0	0.7	0	0	0.5	0	0	A
<i>Oxudercus dentatus</i> (Ox.de)	0	0.5	0	0.3	0	0	0	0.8	0	0	0	0	0	0.3	0.4	0.5	0.2	0.2	ES
<i>Periophthalmus novemradiatus</i> (Pe.no)	4.8	0	0	2.7	0.2	0.4	7.2	0	0	77.8	87.2	87.3	59.4	62.8	62.7	58.9	69.8	81.1	ES
<i>Pseudapocryptes elongatus</i> (Psp.el)	1.8	0	0.7	6.4	14.4	3.0	1.2	16.9	0	5.8	6.4	5.0	11.6	16.4	16.8	3.5	6.5	6.8	ES
<i>Pseudorhombus javanicus</i> (Psd.ja)	0	0.7	0	0	0	1.4	0.2	0.4	0.1	0	0	0	0	0	0	0	0	0	ES
<i>Scatophagus argus</i> (Sc.ar)	0.6	0	1.7	0	0	0.1	1.4	5.0	0	0	0	0	0	0	0	0	0	0	ES
<i>Setipinna taty</i> (Se.ta)	3.2	1.2	0	0	6.1	7.8	3.0	8.2	10.7	0	0	0	0	0	0	0	0	0	MM
<i>Sillaginopsis panigus</i> (Si.pa)	4.2	0.2	0	0	0	0	0.2	0.2	0	0	0	0	0	0	0	0	0	0	ES
<i>Strongylura strongylura</i> (Str.st)	0	0	0.1	0	1.2	0.5	0.5	1.0	0	0	0	0	0	0	0	0	0	0	ES
<i>Strophidon sathete</i> (Stp.sa)	0	0	0	0	0.1	0	0.2	0.8	0	1.4	0	0	1.4	0	0.7	0.9	0	0	ES
<i>Taenoides buchamani</i> (Ta.bu)	0	0.2	0	0	0	0	0.2	0.6	0	0	0	0	0	0	0	0	0.7	1.1	ES
<i>Terapon jarbua</i> (Te.ja)	0	0	1.3	2.4	4.4	1.0	1.6	3.0	0.1	0	0	0	0	0	0	0	0	0	C
<i>Toxotes chatareus</i> (To.ch)	0	12.8	0	0	0.2	0	0.7	0	0	0	0	0	0	0	0	0	0	0	ES
<i>Trichurus gangeticus</i> (Tri.ga)	0	21.6	0.3	3.0	2.0	14.9	9.0	17.1	20.2	0	0	0	0	0	0	0	0	0	MM
<i>Trypauchen vagina</i> (Try.va)	0.6	0	0.3	0	0.4	0	0	1.2	0	1.1	0	0	1.4	2.0	0	1.4	1.9	0.5	ES
<i>Uroconger lepturus</i> (Uroc.le)	0.6	0	0	0	0.1	0	0	0.4	0	1.1	0	0	0.7	0	1.4	1.4	0	0	MM
<i>Uropterygius marmoratus</i> (Urop.ma)	0	0	0.2	0.3	0	2.5	0.5	2.0	0.1	0	0	0.7	2.9	4.1	4.3	1.1	0.6	0.2	ES

of a year, as well as between years for a particular season.

A total of 4891 individuals were collected, representing 31 species from 22 families and 9 orders (Table 2). Both tidal conditions showed a seasonal pattern in diversity values and ecological guilds. The monsoon and post-monsoon seasons showed significantly higher species diversity (H'), evenness (J), species richness (S) and lower species dominance (D) (p=0.000) than the pre-monsoon season (Fig. 2) during high-tide sampling. This trend was maintained in all three consecutive years. The diversity indices also varied significantly between years in a particular season. However, the diversity attributes were found to be lower for all seasons during the third year than in the two preceding years. Similarly, during low tide conditions, H', S, J and D were found to be significantly different (p=0.000) between three respective seasons and monsoon was found to be the most diverse season throughout the study period. Diversity was significantly high (p=0.000) in the first year for all three seasons during low-tide conditions.

Cluster analysis data based on species abundance of three seasons in three years at high tide and low tide illustrated a clear division of fish assemblage into four distinct groups (55% Bray-Curtis similarity) (Fig. 3A). The dendrogram pattern was well supported by nMDS results, which showed considerable distances between four groups (stress value =0.05) (Fig. 3B). One group was composed of three seasons of three years at low tide, the second was composed of the monsoon and post-monsoon seasons of the third year at high tide, and the third group was composed of the pre-monsoon season of the first and third year and the monsoon and post-monsoon seasons of the first (60% Bray-Curtis similarity) and second year (60% Bray-

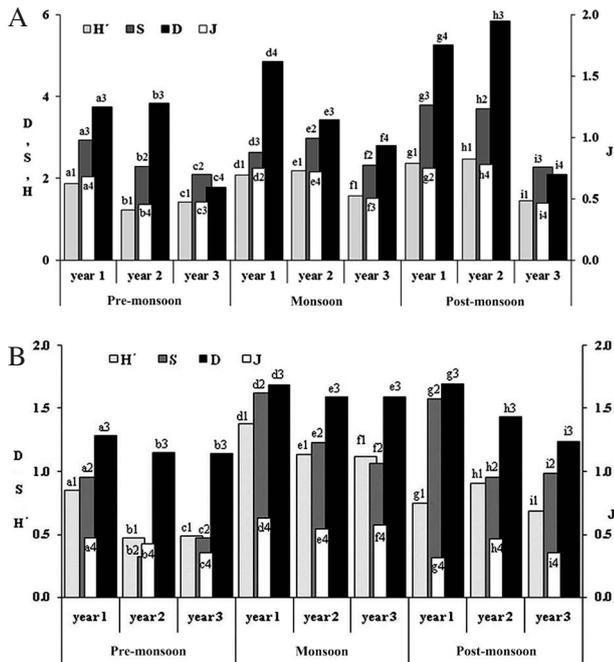


FIG. 2. – Seasonal and inter-annual variation of Shannon-Weiner (H'), species richness (S), Pielou evenness (J) and species dominance (D) indices for mudflats at high tide (A) and low tide (B). N.B.: Different letters with different numbers indicate significant differences at 0.05% level of significance.

Curtis similarity) of high tide. The last group was only represented by the pre-monsoon season of the second year at high tide. No significant differences were observed from ANOSIM in the community structure in three seasons and in three years during high-tide and low-tide conditions.

Five ecological guilds were identified during high-tide and low-tide conditions when three seasons (pre-monsoon, monsoon and post-monsoon) of three years were considered. Ecological guilds were analysed by number of species within each guild and 18 estuarine species were found from the 31 species identified in the present study. With regard to the percentage abundance of individuals contributing each ecological guild, one-way ANOVA showed significant differences ( $p=0.05$ ) between seasons in each year and between years for each season during ebb tide, as shown in Figure 4A. When seasons were compared, ES and MM were found to be the highest in percentage of individuals in the monsoon and post-monsoon seasons, respectively, whereas, F and C represented maximum abundance during the pre-monsoon season. A significantly higher percentage abundance of A was recorded in the pre-monsoon season than in the other seasons in every year. In terms of species contribution for each guild, there were significant differences between seasons of each year and between years of a particular season in high-tide conditions (Fig. 4A). The highest percentage of species within ES and F guilds was recorded in the post-monsoon season, whereas this percentage for A was higher in the pre-monsoon season of all three years studied.

A similar trend was also observed at low tide, though no species of F and C species were captured in any seasons of any year and ES contributed the highest percentage of individuals as well as the highest percentage of species throughout the years (Fig. 4B).

The CCA analysis for fish assemblage (based on 432 samples in each tidal phase, including all seasons in the study period) indicated that the variables (abiotic and biotic) explain significantly about 83.5% (considering a cumulative percentage variance of four axes) and 93.2% (considering a cumulative percentage variance of four axes) of the fish assemblages during high tide and low tide. Although several axes were determined within the analysis, only axes 1 and 2 were plotted as they accounted for 60.9% and 81.5% of the variability explained by four axes for high tide and low tide, respectively.

Considering their vector length pH ( $r=0.46$ ), inorganic phosphate ( $r=-0.40$ ), nitrate nitrogen ( $r=-0.64$ ), nitrite nitrogen ( $r=-0.50$ ) (best correlated with axis 1) and salinity ( $r=0.42, 0.43$ ) (best correlated with axis 1 and axis 2) were the most important environmental variables influencing the fish assemblages at high tide (Fig. 5A). On the other hand, water temperature ( $r=0.33$ ), total dissolved solids ( $r=-0.34$ ) (best correlated with axis 1) and salinity ( $r=0.25, -0.20$ ) (best correlated with axis 1 and axis 2, respectively) were

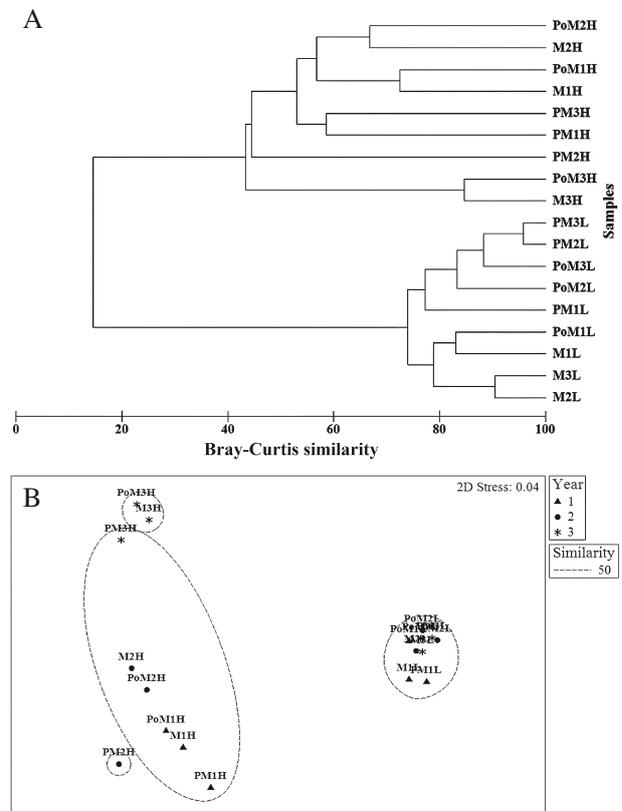


FIG. 3. – Cluster analysis (A) and two-dimensional nMDS plot (B) of the fish assemblages (based on fish abundances) according to Bray-Curtis similarity. Stress value (2D): 0.04.

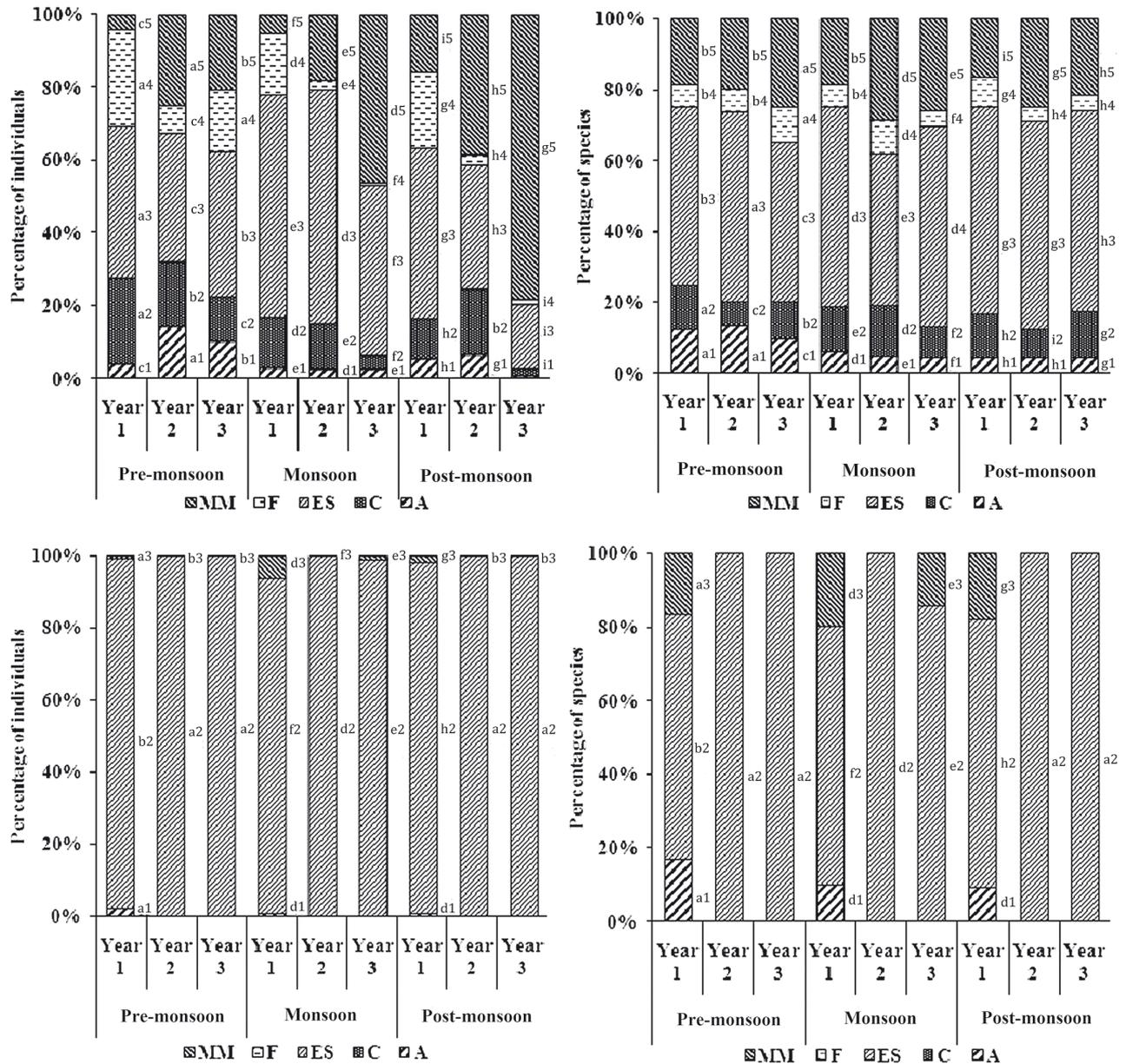


Fig. 4. – Seasonal and inter-annual percentage of ecological guilds for mudflats at high tide (A) and low tide (B) by species composition. Different letters with different numbers indicate significant differences at 0.05% level of significance.

the most important environmental variables influencing the fish assemblages at low tide (Fig. 5B). During high tide, axis 1 separated the species sensitive to pH variations (on the right) from those preferring nutrient-rich environments (containing nitrate nitrogen, nitrite nitrogen and inorganic phosphate) (on the left), whereas both axes separated the species encountered with higher salinity (in the upper half) from those having lower salinity tolerance (in the lower half). Likewise, during low tide, temperature and total dissolved solids played an important role in classifying species according to axis 1, though axis 2 separated the species having an affinity for salinity (in the upper half) from those sensitive to it (in the lower half) (Fig. 5B).

## DISCUSSION

Estuarine intertidal mudflats are very important in the functioning of estuarine systems and it is generally recognized that they have a disproportionately high productivity when compared to subtidal areas (Elliott and Dewailly 1995). These sheltered shallow waters provide important feeding grounds for juvenile fishes (Haedrich 1983, Able *et al.* 1990, Costa and Elliott 1991). Little work has been done about the nekton communities that use mudflat habitats. The processes related to the use of these areas by highly mobile individuals like fish are still largely unknown. As the mudflats totally drain during the ebb, the majority of

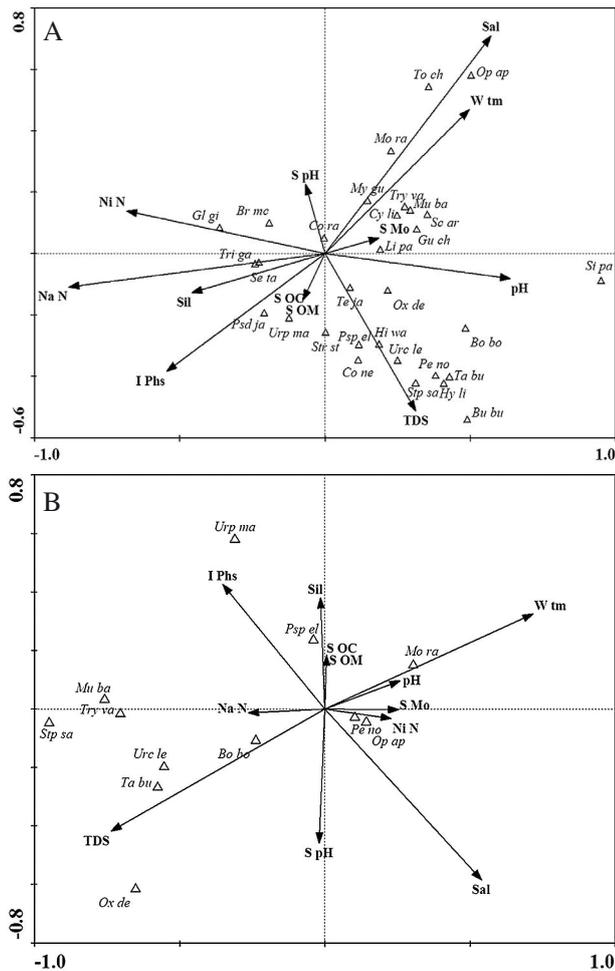


Fig. 5. – Canonical correspondence analysis (CCA) ordination diagram based on species abundances, with abiotic environmental factors represented by vectors in high-tide (A) and low-tide (B) conditions. Variable abbreviations are given in Tables 1 and 2.

the fish species can only migrate when the rising tide floods the intertidal flats (Vinagre *et al.* 2006).

In the present study 12 species of fishes were recorded in low-tide and 31 species in high-tide conditions. The number of fish species recorded in the studied mudflat during high tide was higher than in other geographical areas, as recorded in previous studies: 22 fish species were recorded on the mudflats of Tagus estuary (Salgado *et al.* 2004), 17 fish species on an intertidal mudflat of an Australian estuary (Morrison *et al.* 2002), 20 in an intertidal mudflat of an estuarine system in Japan (Kanou *et al.* 2005) and 18 in France (Amara and Paul 2003).

The transient nature of many species is a major characteristic of an estuarine fish population that influences diversity. High diversity and species richness is a characteristic feature of subtropical and tropical estuaries of the Indo-Pacific region (Blaber *et al.* 1989). Emigration and immigration of fish can directly affect the population diversity. In the present study, all diversity indices showed marked seasonal variations, and at

high tide the drop in  $H'$  during the pre-monsoon season regardless of the years (Fig. 2) was directly attributable to the exodus of eight of the studied species (*B. butis*, *C. neglecta*, *H. limbatus*, *O. dentatus*, *S. strongyula*, *S. sathete*, *T. buchani* and *U. marmoratus*). The occurrence of mainly three estuarine species, *M. raitaborus*, *S. panigus* and *T. chatareus*, and the immigration of the anadromous species *O. apicalis* occurred during the period. The rise in  $H'$  in the monsoon and post-monsoon seasons was primarily a result of the immigration of various marine migrant fish species. The result corroborated the study by Mondal *et al.* (2010) in two flood plain lakes of India. A similar trend was observed for species richness. On the other hand, during the warm-rainy season (July-September), precipitation and elevated plant production act in concert to contribute allochthonous organic matter (detritus) and nutrients via river discharges and run-off from the lagoon basin, so increasing availability of trophic resources (Castillo-Rivera *et al.* 1994) leads to higher species diversity. The assemblage groups revealed from the nMDS analysis were clearly separated in the present study according to tidal influence, and to a lesser extent, according to seasonal and inter-annual basis. The high dominance of a few non-commercial species/taxa (*P. novemradiatus*, Gobiidae), widely distributed in exposed mudflats at low tide during the pre-monsoon season, was also reflected by the low diversity values. In contrast, for some tropical estuarine systems, a higher number of species had been reported in the mudflat habitat than in the adjacent mangrove area (Hindell and Jenkins 2004).

The estuarine fish assemblages were also defined through the use of functional guilds. Functional guild analysis has been proposed as an alternative or addition to traditional community analysis because it can provide more information on the functioning and the internal and hierarchical structure of fish communities (Franco *et al.* 2006), as well as values for metrics to describe aspects of habitat use by fish (Elliott and Dewailly 1995, Mathieson *et al.* 2000). Most of the studies using functional guilds aim either to describe the fish assemblage composition of a single estuary or to compare fish assemblages across different estuaries, without taking into account tidal and seasonal differences within a single habitat of the estuary. Fish assemblages in European estuaries are typically dominated by either migrant or straggler marine species, i.e. irregular visitors with no apparent estuarine requirements (Elliott and Dewailly 1995, Thiel and Potter 2001, Maes *et al.* 2005, Pombo *et al.* 2007, Franco *et al.* 2008, Cabral *et al.* 2012).

The fish assemblage structure of the mudflats of Sundarbans at high tide and low tide consisted of ecological guilds that are quite common in European estuaries (Franco *et al.* 2008). Estuarine species (43.0%-58.0% during high tide and 66.7%-72.7% during low tide) were the most important ecological guild of the mudflats of Sundarbans, mainly belonging to

the orders Clupeiformes and Perciformes. Significant seasonal (except catadromous for the first year) and inter-annual variations in five ecological guilds were observed due to migration of some fishes during high tide. However, the seasonal effect was negligible in the low-tide environment.

At the species level the fish fauna was largely dominated by *P. novemradiatus* at low tide throughout the study tenure, whereas *G. chapra*, *T. gangeticus* and *C. ramcarati* were dominant in the first year during three respective seasons at high tide. In the second year the two species of *Coilia* showed maximum dominance throughout the year. However, in the last year in high-tide conditions the fish assemblage was dominated by *G. chapra*, *L. parsia* and *B. mccllellandi* in the pre-monsoon, monsoon and post-monsoon seasons, respectively. The fact that the largest proportion of ES was found in the mudflat habitat suggested that this habitat might play an important role as a suitable feeding ground for several fish species (Nanjo *et al.* 2008, Chaudhuri *et al.* 2012). In the last two years of the study period the percentage abundance of MM individuals (e.g. *B. mccllellandi*, *S. taty*, *T. gangeticus*) increased ( $p > 0.000$ ) compared with the other ecological guilds during high tide, possibly due to the effect of a catastrophic cyclone in the year 2009 (Mukherjee *et al.* 2012).

The evident rise in salinity with a concomitant increase in temperature in the later phase of the study period explained the noticeable increase in the marine migrant species during high tide. It also suggests the probable cause of the shift of the fish assemblage composition. However, despite the recognized importance of mudflats as nursery areas (van der Veer *et al.* 2001, Morrison *et al.* 2002, Amara and Paul 2003, Vinagre *et al.* 2006), some controversy exists as to whether or not marine fish species are really dependent on estuaries or just use them opportunistically in order to achieve higher growth rates and a lower exposure to piscivorous predation than is found in other inshore coastal areas (Paterson and Whitfield 2000).

In some geographic areas, sheltered estuarine habitats may offer high densities of prey and other food not encountered in marine areas, and their turbid shallow waters provide protection from predators (McLusky and Elliott 2004). The simultaneous use of estuarine and shallow marine habitats may be a strategy to reduce the intra- and interspecific competition (for food or space), particularly during peak recruitment (Amara *et al.* 2001). Individual fish may quickly respond to climatic constraints or an increased mortality risk and rapidly shift between coastal and estuarine nursery areas in order to increase their individual state and fitness (Childs *et al.* 2008).

Understanding the relationship between species distribution and environmental variables allows us to identify the ecological processes that regulate different populations and communities in ecology. However, in addition to all the changes in environmental condi-

tions, many species change their habitats according to their ontogeny or seasonal rhythms, which means that relations between different species and their environment or habitat are spatially and seasonally dynamic (Morrison *et al.* 2002, Kanou *et al.* 2005).

Several estuarine studies have emphasized the importance of environmental factors affecting seasonal and spatial changes in fish and macrocrustacean assemblage structure (Blaber and Blaber 1980, Rakocinski *et al.* 1996, Gelwick *et al.* 2001). The fish assemblage and species composition of the mudflats of Sundarbans is influenced seasonally by a variety of factors. In the present study, nutrients of water, pH and salinity influenced the assemblage pattern significantly during ebb tide, whereas water temperature, total dissolved solids (TDS), and salinity were the most important environmental variables influencing species richness, abundance and fish assemblage in the intertidal mudflats of the Sundarbans at low tide. The TDS test measures the amount of particles that are dissolved in water. TDS in excessive amounts may be unsuitable for aquatic life. Seasonal analysis revealed that TDS values were low in winter and high in summer and the monsoon season. Similar results were reported by Narain and Chauhan (2002) and Helms *et al.* (2009). During low tide two estuarine species (*T. buchanani* and *O. dentatus*) and one marine migrant species (*U. lepturus*) showed strong correlation with total dissolved solids. Most of the fishes showed negative correlation with salinity and temperature. Thiel *et al.* (1995) found temperature to be the best predictor of temporal changes in fish abundance and species composition in the Elbe estuary, Germany. Temperature has been identified as the primary abiotic factor controlling key physiological, biochemical and life-history processes of fish (Beitinger and Fitzpatrick 1979) and has been found to influence the utilization of estuaries by fish worldwide (Blaber 2000, Thiel *et al.* 1995, Harrison and Whitfield 2006, Nip and Wong 2010). Generally, fish have a thermal preference that optimizes physiological processes.

In the present study salinity was an important factor profoundly influencing the seasonal abundance and distribution of fishes in estuarine environment. The lower salinity was recorded during monsoon was due to heavy rainfall and a large quantity of fresh water inflow. Similar observations were recorded by Kannan and Kannan (1996), Satpathy (1996) and Soundarapandian *et al.* (2009). The anadromous *O. apicalis* and the estuarine species *T. chatareus* showed an affinity towards salinity during high tide, whereas *S. panigus* may have benefited from a wider pH tolerance in contrast to *P. javanicus*, *G. giuris*, *T. gangeticus* and *S. taty*, which preferred a nutrient-rich environment during high-tide conditions.

pH showed well-marked seasonal variation in the present study, and higher values of pH were recorded during the pre-monsoon months (average of three years: 7.4). Ananthan *et al.* (1992) stated that the higher value of pH in summer was due to the uptake of CO<sub>2</sub>

by photosynthesizing organisms. In the present study, pH showed associations with fish distributions similar to those of other estuarine systems (Maes *et al.* 1998, Whitfield 1999). *S. panigus* showed a positive correlation with pH, whereas the group of fishes *G. giuris*, *T. gangeticus*, *S. taty* and *P. javanicus* showed affinity for nutrient rich-environments containing nitrate nitrogen, nitrite nitrogen and inorganic phosphate. Dissolved nutrient concentrations were described as the best predictors of species diversity and fish abundance by Winemiller *et al.* (2000).

Throughout this study, seasonal and inter-annual variations were found in all of the approaches used to analyse fish assemblages: diversity, species compositions and ecological guild distribution. Overall, the low diversity found in the pre-monsoon season was in contrast with the study by Cardoso *et al.* (2011) in the Portuguese coasts. Estuarine species had higher relative abundances in winter in both high- and low-tide conditions. A similar seasonal pattern was observed for estuarine resident species in the other studies in different European estuaries (Blaber and Blaber 1980, Pombo *et al.* 2007, França *et al.* 2008, Selleslugh and Amara 2008). This seasonal pattern allows the use of the mudflats of the Sundarbans to be considered as contributors to the support of coastal fish populations because they contain temporary habitats that provide shelter and feeding grounds to the critical life stages (Cardoso *et al.* 2011) of many species.

The results of the present study emphasized the importance of this mudflat habitat in the Sundarbans estuary for the nekton communities. Many of the species captured seem to benefit from the advantages of the intertidal habitat, and particularly the high availability of food (Chaudhuri *et al.* 2012). Further studies about this intertidal mudflat and the communities are crucial in order to understand its structure, dynamics and relation to other estuarine habitats.

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