

Species composition and size distribution of the tropical estuarine fishes in Matang Mangrove Forest Reserve (MMFR), Malaysia

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Abstract. Zuraini MI, Kadir STSA, Sobri MFM, Muda AM, Abdurahman SW, Hassan N, Jaaman SA, Abdullah MM. 2026. Species composition and size distribution of the tropical estuarine fishes in Matang Mangrove Forest Reserve (MMFR), Malaysia. *Biodiversitas* 27 (1): d270137. <https://doi.org/10.13057/biodiv/d270137>. The Matang Mangrove Forest Reserve (MMFR) in Perak, Malaysia, represents one of the most well-managed and ecologically significant mangrove ecosystems in the world. Spanning over 40,000 ha and protected since 1906, MMFR provides critical nursery and feeding habitats for a wide range of marine fauna, including commercially important fish, crustaceans, shellfish, and endangered marine cetaceans. This study was conducted to determine the diversity, composition and size distribution of estuarine fishes in three estuaries connected to the MMFR namely Kuala Larut (KL), Kuala Sangga (KS) and Kuala Gula (KG). Samplings were conducted in October, November and December 2021 using gill nets that were deployed along the estuarine gradients at the upper (near riverine areas), the middle, and the mouth (near the coastal interface) estuary. A total of 2,756 fish individuals, representing 42 species across 21 families, were collected. The most abundant family was Engraulidae (N: 1,400), dominated by *Thryssa kammalensis* by 49.96%, followed by the family Mugilidae (N: 504), primarily composed of *Paramugil parmatus* by 14.77%, and Ariidae (N: 457), dominated by *Arius maculatus* by 10.19%. The Shannon diversity index (H') was highest at KL (2.12), followed by KS (1.63) and KG (1.35), with Pielou's evenness index (J') mirrored this trend. Meanwhile, species richness is highest at KS, followed by KL and KG, indicating heterogeneity in community composition among estuaries. The presence of three Near Threatened (NT) species listed by the IUCN, namely *Protonibea diacanthus*, *Brevitrygon walga* and *Arius gagora*, underscores the ecological significance of the estuarine habitats within the MMFR. This study provides an updated baseline data on fish diversity in MMFR, offering critical insights to guide future conservation planning and sustainable resource management.

Keywords: Ariidae, diversity indices, Engraulidae, estuarine ecology, fish distribution, Mugilidae

INTRODUCTION

Mangrove ecosystems play a pivotal role in supporting coastal fisheries by serving as critical habitats of biodiversity that provide trophic resources, physical refuge, and larval retention for a wide range of marine organisms, many of which are commercially important species that later migrate and thus, underpins coastal productivity (Kiso and Mahyam 2003; Nagelkerken et al. 2008; Kadir et al. 2019; Abidin et al. 2021). Malaysia's mangroves are believed to contribute to over 50% of the country's annual offshore fishery landings, which total approximately 1.28 million tons (Chong 2007). This statistic underscores the immense economic and ecological value of mangrove forests, particularly in sustaining artisanal and commercial fisheries across coastal landscapes. However, mangroves continue to face many threats including habitat destruction due to aquaculture, urban expansion, and coastal development, overfishing and aquaculture pollution, intensifying the

urgency for updated biodiversity assessments linked to fisheries (Lei et al. 2022). Such assessments are increasingly important because fish communities respond rapidly to environmental change and can reveal early signs of ecosystem degradation.

The Matang Mangrove Forest Reserve (MMFR) in Peninsular Malaysia is one of the world's largest and longest-managed mangrove forests. Established in 1902 and located in the state of Perak, MMFR is widely recognized for its globally exemplary, sustainable management practices, balancing timber production with ecosystem conservation (Goessens et al. 2014). It is considered one of Peninsular Malaysia's most intensive fishery grounds, sustaining both local livelihoods and regional seafood supplies. The fisheries sector within MMFR generates million ringgits of annual revenue from crabs, prawns, and fish harvests, emphasizing its role as a significant contributor to local livelihoods and regional economy. In addition to its critical role for fisheries, the MMFR serves as a key foraging

ground for marine cetaceans, including the Irrawaddy dolphin (*Orcaella brevirostris*), Indo-Pacific finless porpoise (*Neophocaena phocaenoides*), and Indo-Pacific humpback dolphin (*Sousa chinensis*) (Kuit et al. 2019; Kuit et al. 2021; Sobri et al. 2022). These cetaceans are sighted year-round in the shallow estuarine waters and mudflats of MMFR, sustained by rich fisheries and diverse marine life that provide a reliable prey base. These interactions underscore the ecological interconnectedness of estuarine productivity and marine megafauna conservation at MMFR, and they further highlight the value of maintaining fish diversity and abundance within the reserve.

Despite its reputation as one of the best-managed mangrove systems globally (Jusoff 2000; Goessens et al. 2014), MMFR is increasingly challenged by habitat loss from aquaculture and industrial development, as well as pollution from anthropogenic sources (Ibharim et al. 2015; Salam et al. 2020). Ibharim et al. (2024) reported extensive land conversion in the MMFR, with 4,625.1 ha (16.7%) converted to water bodies, 1,886.1 ha (6.8%) transformed into dryland forest, and 186.9 ha (0.7%) converted to oil palm plantations. Tropical mangroves are essential in supporting diverse fish assemblages (Al-Jufaili et al. 2021; Lei et al. 2022; Wickramasinghe et al. 2022; Aransiola et al. 2024; Ram et al. 2025; Wahyudewantoro et al. 2025), highlighting consistent mangrove-fishery linkages. In estuarine environments like MMFR, which support both artisanal and commercial fisheries, key fish species may serve as indicators of habitat health and productivity (Blaber 2000; Nagelkerken et al. 2008), reinforcing the importance of fish assessment. Addressing this gap is vital because dominant and abundant species not only regulate ecosystem dynamics but also determine the sustainability

of fishery yields that coastal communities depend upon. This study aims to determine the species composition and relative abundance of estuarine fishes in MMFR, with particular attention to identifying dominant taxa. The findings establish a contemporary benchmark for comparing MMFR with other mangrove systems worldwide and provide an evidence base to guide sustainable fisheries management and biodiversity conservation in Malaysia's most ecologically significant mangrove reserve.

MATERIALS AND METHODS

Study area

The MMFR in Perak, Peninsular Malaysia, is a vast crescent-shaped coastal strip that extends approximately 51.5 km from Kuala Gula to Bagan Panchor and spans up to 13 km in width at its broadest point (Figure 1). Encompassing over 40,000 ha, MMFR is recognized as the largest mangrove forest reserve in Peninsular Malaysia (Khan et al. 2024). The area is intersected by an extensive network of mangrove waterways, and mudflats dominate the shoreline and spaces between islands adjacent to the forest. The extensive network of rivers and waterways within the MMFR supports its utilization for aquaculture, particularly as nursery grounds for commercially valuable species such as fish and prawns. Furthermore, 74.8% of the area is gazetted for economic purposes (such as timber and charcoal production), while the remaining 25.2% is designated as protected or non-productive forest, highlighting the economic importance of the MMFR (Sasekumar et al. 1994; Chong 2006; Chew et al. 2007; Zulfa et al. 2021).

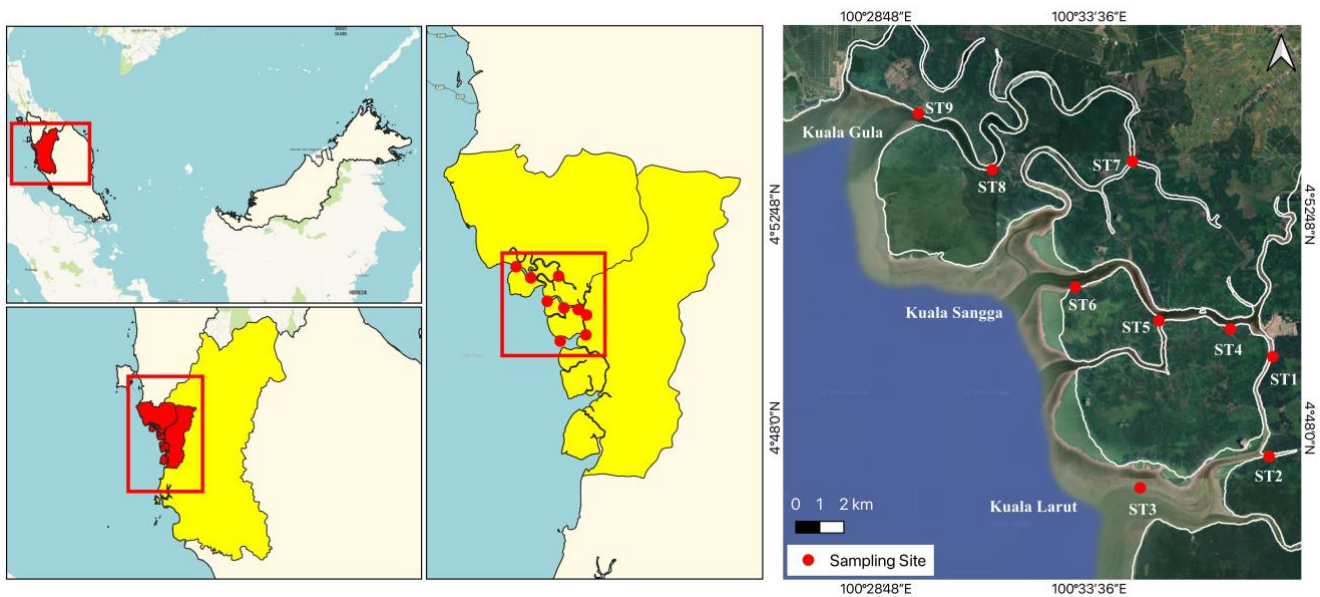


Figure 1. Map of the Matang Mangrove Forest Reserve (MMFR), Malaysia, showing the nine sampling sites distributed across three estuaries: ST1-ST3 located in the southern estuary (Kuala Larut), ST4-ST6 in the central estuary (Kuala Sangga), and ST7-ST9 in the northern estuary (Kuala Gula) surrounded by mangroves within the MMFR

Fish sampling

Samplings for fishes from the three mangrove estuaries of MMFR, namely Kuala Larut (KL), Kuala Sangga (KS) and Kuala Gula (KG), were conducted using gillnet in October and December 2021. The gillnet used was made of nylon net lengths up to 30 m and 2 m height, with three mesh sizes at 1, 3 and 5 inches to capture a broad range of fish sizes and species, thereby reducing size selectivity bias and ensuring a more comprehensive species composition. A series of floats tied to the top edge and weights anchored to the bottom edge were used to set the gillnet in a vertical orientation from the surface to the deeper parts of the mangrove areas. At each estuary, the gillnets were deployed at three distinct zones following the estuarine gradient at the upper estuary (near riverine areas), the middle estuary, and the estuary mouth (near the coastal interface), to account for This stratified approach ensured that resident, transient, and migratory species across the full estuarine continuum are adequately represented, as fish communities often vary along salinity, turbidity and habitat transitions (Whitfield 1999; Elliot et al. 2007). Gillnets were deployed during high tide and retrieved after a fixed soak time of 2 hours. The procedure was replicated in the subsequent tidal cycle to ensure sampling across both diurnal and nocturnal periods. This strategy allowed effective capture of fishes moving with the tidal flow, thereby accounting for diel and tidal variations within the estuary.

In total, six net deployments were conducted, amounting to 12 hours of soaking time at each estuary (KL, KS, KG). All captured specimens were promptly collected and transported for identification and counting. Data for water parameters were collected using HI98195 Multiparameter pH/ORP/EC/Pressure/Temperature Waterproof Meter supplied with HI7698195 probe with 4 m cable from Hanna Instruments. To maintain freshness, fish samples were kept on ice during transportation and identification. Specimens were classified to family and species levels based on morphological characteristics, after which each individual was measured for total length (TL), standard length (SL), and fork length (FL) to the nearest 1 mm, and weighed to the nearest 0.01 g. For rays, disk width (DW) measurements were taken. Three individuals from each species were selected for photographic documentation, and the specimens were gently covered with wet tissue paper to prevent physical damage during photography. Before imaging, the fins were carefully spread using pins, and the specimens were briefly fixed in 10% formalin for approximately 5 minutes to preserve fin structure and overall morphology. The fishes were then fixed in 10% formalin solution and subsequently preserved in 70% alcohol for long-term storage. Fish species were identified based on several publications (Mansor 1998; Matsunuma et al. 2011; Lim et al. 2018; Motomura et al. 2021; Seah et al. 2021) and FishBase (Froese and Pauly 2025).

Data analysis

Diversity indices

The abundance data were further analyzed for diversity, species richness, and evenness indices using PRIMER v7 software (Clarke and Warwick 2001). Shannon-Wiener

index was used to describe community complexity, while species richness reflects the total number of species present, indicating the habitat's capacity to support biodiversity. Evenness indices measure the uniformity of individual distribution among species, which is critical for detecting dominance patterns often observed in estuarine and mangrove systems. Together, these indices enable robust assessment of the ecological condition of MMFR's fish community and facilitate comparisons with other studies. The indices were measured using formula as follows:

Shannon diversity index:

$$H' = -\sum(\pi_i \times \ln(\pi_i))$$

Where, S: Total number of species, π_i : The ratio of the total number of individuals.

Margalef index (species richness):

$$d = (S-1)/\log(N)$$

Where, S: Total number of species, N: Total number of individuals of all species.

Pielou's evenness index:

$$J' = H' / \ln(S)$$

Where, H' : Diversity index, S: Total number of species, \ln : Normal log.

Species accumulation curve analysis

To assess sampling sufficiency and estimate species richness, a species accumulation curve (SAC) was constructed using non-cumulative data on the number of individuals and the corresponding number of species observed from gillnet samples. The curve was fitted with the Michaelis-Menten model, a widely used asymptotic function in ecological studies that describes species richness as increasing rapidly with initial sampling effort before gradually approaching an asymptote, the point at which additional sampling yields few or no new species, thus providing a biologically realistic estimate of total species richness (Gotelli and Colwell 2001). The model is described by the equation:

$$S_{(x)} = S_{\max}(x) / (K + x)$$

Where, $S_{(x)}$: Expected number of species at sampling effort x , S_{\max} : Estimated maximum number of species (asymptote), K: Number of individuals at which half of S_{\max} is reached.

Length and weight frequency distributions

The length and weight frequency distributions of the eight most abundant species namely *Thryssa kammalensis*, *Paramugil parmatus*, *Arius maculatus*, *Hexanematichthys sagor*, *Planiliza subviridis*, *Anodontostoma chacunda*, *Pennahia aneus*, and *Escualosa thoracata* were examined across all sampling estuaries (Figure 5 and 6).

Statistical analysis

Canonical correspondence analysis (CCA) was employed to examine the relationships between fish assemblage composition and environmental variables. This method

extracts canonical axes (eigenvectors) that maximize the proportion of variance in species composition explained by the environmental variables. Fish abundance data were transformed using the Hellinger transformation to reduce the influence of dominant species and to make the data suitable for ordination analysis. Environmental variables were standardized using the z-score transformation to allow comparison among variables with different units. The first two canonical axes (CCA1 and CCA2) were used to construct biplots showing species environment relationships. Significance of the canonical axes and individual environmental variables was assessed using a Monte Carlo permutation test (999 permutations, α : 0,05). Statistical analyses were performed in R version 4.5.1 (R Core Team, 2025) using RStudio (Posit Software, version 2025.05.1 + 513). Differences in diversity indices among upper, middle, and mouth estuary zones were tested using the Kruskal-Wallis non-parametric test due to small sample sizes and non-normal data distribution. The test compares median values among groups based on ranked data, with significance assessed at α : 0.05.

RESULTS AND DISCUSSION

Water parameters

Salinity values varied across the estuarine gradient. Stations located at the upper estuaries (ST1, ST4, ST7) recorded the lowest salinity levels, ranging from 12.78 to 18.07 PSU. Salinity increased in the middle estuaries (ST2, ST5, ST8), with values ranging between 17.15 and 21.93 PSU. The highest salinity was recorded at the mouth of the estuaries (ST3, ST6, ST9), ranging from 20.96 to 26.05 PSU. This pattern reflects the typical estuarine transition from freshwater-dominated upstream areas to more marine-influenced downstream zones. Water temperature remained relatively uniform across all stations, ranging from 29.77°C to 32.36°C, suggesting minimal spatial variation in thermal conditions during the sampling period. In contrast, pH, dissolved oxygen (DO), and turbidity exhibited notable variability among zones and estuaries. Turbidity tended to be higher at upstream zones, reflecting greater freshwater and sediment input, while pH and DO were generally

higher in downstream and more marine-influenced zones. Overall, these gradients in salinity, turbidity, pH, and DO illustrate the ecological transition typical of estuarine systems, from river-dominated, turbid freshwater inputs upstream to more saline, oxygen-rich, and stable conditions near the estuary mouths (Table 1).

Fish composition and abundance

A total of 2,756 fish individuals, representing 42 species from 21 families, were recorded across the three sampled estuaries of the MMFR. Diversity metrics showed clear spatial variation. The Shannon diversity index (H') was highest at KL (2.12), followed by KS (1.63) and KG (1.35). Pielou's evenness index (J') mirrored this trend, with values of 0.64, 0.48, and 0.42, respectively. In contrast, Margalef's species richness index (D') peaked at KS (29.85), followed by KL (27.85) and KG (23.86), indicating heterogeneity in community composition among estuaries. However, no significant differences were detected in any of the ecological indices among upper, middle, and mouth estuary zones (Kruskal-Wallis test, $p > 0.05$ for all indices), indicating high within-zone variability and weak zonal structuring of fish diversity (Table 2).

The species accumulation curve (SAC) demonstrated a clear relationship between the number of individuals collected and the cumulative number of species recorded (Figure 2). The curve rose steeply at the beginning of the sampling sequence, indicating frequent encounters with new species as sampling commenced. The rate of species discovery began to stabilize at approximately 400-500 individuals, after which the curve approached an asymptote. This plateau suggests that the majority of species present in the sampled estuaries had already been detected. A slight decline in species count beyond this point reflects repetitive captures of the same species rather than the addition of new taxa, a pattern commonly observed when sampling effort becomes saturated. Collectively, the shape of the SAC indicates that the sampling effort employed in this study was sufficient to capture the dominant components of the fish assemblage and to provide a reliable estimate of species richness within the MMFR estuarine system.

Table 1. Summary of water parameters measured at three sampling sites within the Matang Mangrove Forest Reserve: Kuala Larut, Kuala Sangga, and Kuala Gula. These locations were strategically selected to represent an estuarine gradient from the upper estuary (ST1, ST4, ST7) to the middle (ST2, ST5, ST8) and the mouth (ST3, ST6, ST9)

Parameter	Kuala Larut			Kuala Sangga			Kuala Gula		
	ST1	ST2	ST3	ST4	ST5	ST6	ST7	ST8	ST9
Depth (m)	1.7-1.8	2.1-2.2	1.5-1.6	1.3-2.7	1.5-8.9	2.4-2.9	5.9-8.5	6.6-11.6	2.6-7.8
pH	7.05-7.10	7.26-7.80	7.72-7.90	6.75-6.90	7.03-7.15	7.69-7.83	7.18-7.40	8.13-8.25	8.26-8.30
DO (ppm)	4.45-4.80	6.31-9.98	5.57-7.55	1.94-2.39	3.43-3.81	5.48-7.26	2.95-4.26	6.31-6.60	6.37-6.77
Salinity (PSU)	16.00-17.15	7.15-11.76	24.68-26.05	12.78-18.07	15.3-20.2	20.96-23.21	14.7-14.87	20.67-21.93	22.27-23.05
Temperature (°C)	31.29-31.92	31.93-31.95	31.88-32.36	29.77-30.38	30.07-30.58	30.53-31.16	29.95-30.03	31.29-31.81	31.01-31.67
Turbidity (NTU)	24.32-26.90	11.91-27.31	6.38-15.92	7.33-28.48	6.27-12.48	7.10-15.16	2.47-6.00	6.56-8.00	3.19-8.30

Table 2. Summary of diversity indices measured at three sampling sites within the Matang Mangrove Forest Reserve: Kuala Larut, Kuala Sangga, and Kuala Gula. These locations were strategically selected to represent an estuarine gradient from the upper estuary (ST1, ST4, ST7) to the middle (ST2, ST5, ST8) and the mouth (ST3, ST6, ST9)

Parameter	Kuala Larut			Kuala Sangga			Kuala Gula		
	ST1	ST2	ST3	ST4	ST5	ST6	ST7	ST8	ST9
Number of species	14	15	16	21	23	8	14	16	8
Number of individuals	343	170	184	454	400	77	313	760	55
Shannon (H') Diversity Index	1.05	2.05	1.9	1.67	1.53	0.81	1.74	0.82	1.39
Pielou (J') Evenness Index	0.4	0.76	0.69	0.55	0.49	0.39	0.66	0.3	0.67
Margalef (D') Species Richness Index	13.83	14.81	15.8	20.84	22.83	7.77	13.83	15.85	7.75

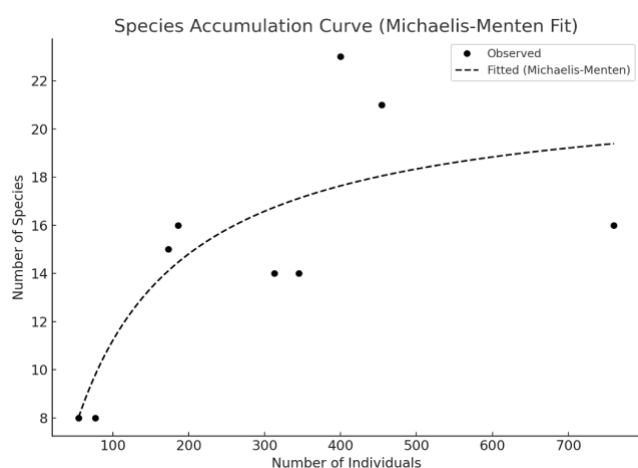


Figure 2. Species accumulation curve fitted with the Michaelis-Menten model for gillnet-caught fish in the estuaries within MMFR

Family-level composition revealed Engraulidae as the most abundant (50.7%), followed by Mugilidae (18.2%), Ariidae (16.5%), Dorosomatidae (4.6%), Sciaenidae (4.4%), Haemulidae (1.6%), with all remaining families contributing 1% and less (Figure 3). Across all estuaries, the most abundant species was *Thryssa kammalensis* (50.0%), followed by *Paramugil parmatus* (14.8%) and *Arius maculatus* (10.2%). Other notable species included *Hexanematichthys sagor* (4.0%), *Planiliza subviridis* (3.5%), *Anodontostoma chacunda* (2.5%), *Pennahia aneus* (2.4%), *Escualosa thoracata* (2.1%), *Pomadasys kaakan* (1.6%), *Johnius macrorhynchus* (1.3%), *Ilisha elongata* (1.1%), and *Scatophagus argus* (1.0%), with all others contributing less than 1% (Table 3).

At KL, *P. parmatus* dominated (39.02%), followed by *T. kammalensis* (11.5%), *P. subviridis* (10.6%), *H. sagor* (9.2%), *E. thoracata* (8.3%), and *A. maculatus* (6.9%). Lesser contributions came from *I. elongata* (2.2%), *Arius venosus* (1.9%), *Glossogobius aureus* (1.6%), *P. kaakan* (1.6%), *Osteogeneiosus militaris* (1.4%), *Thryssa mystax* (1.4%), and *Butis butis* (1.0%), with all other species below 1%. Kuala Sangga was dominated by *T. kammalensis* (59.5%) and *A. maculatus* (14.4%), followed by *H. sagor* (4.6%), *P. parmatus* (4.4%), *P. kaakan* (3.5%), *P. subviridis* (2.1%), *P. aneus* (2.1%), *J. macrorhynchus* (1.6%), and *I. elongata* (1.5%), with other species each contributing less than 1%. KG recorded the highest total fish abundance,

largely due to *T. kammalensis* (65.9%). Other contributors included *A. maculatus* (8.8%), *P. parmatus* (8.3%), *A. chacunda* (5.8%), *P. aneus* (4.1%), *S. argus* (1.6%), *J. macrorhynchus* (1.5%), and *Cryptarius truncatus* (1.2%), with all other species below 1% (Table 2).

Overall, Engraulidae, Mugilidae, and Ariidae were the three most abundant families across estuaries, with Engraulidae showing clear dominance. Kuala Larut, despite having the highest diversity, showed the lowest overall abundance and was strongly dominated by Mugilidae (*P. parmatus* and *P. subviridis*), and the relatively low contribution of Engraulidae suggest a more freshwater-influenced community. Kuala Sangga displayed the highest family diversity, with a balanced distribution among Engraulidae, Ariidae, Mugilidae, Clupeidae, and Sciaenidae. The occurrence of *A. maculatus*, *H. sagor*, and *A. chacunda* reflects the ecological complexity of this mid-estuary environment, influenced by both freshwater and marine inputs, while the exclusive presence of Sciaenidae (*P. aneus*) points to greater habitat heterogeneity (Figure 4). In contrast, KG, while supporting the highest overall abundance, had moderate family diversity dominated by Engraulidae, indicating a community more strongly shaped by marine or coastal influences and with a less structurally complex assemblage compared to Kuala Sangga.

Size distributions

Thryssa kammalensis exhibited a pronounced unimodal weight-frequency distribution, with most individuals weighing 6.5-8.5 g and a peak at 7.5 g. The corresponding length-frequency distribution was similarly bell-shaped, with the majority of fish measuring 9.0-10.5 cm TL, peaking at 10.0 cm. The weight-frequency distribution of *P. parmatus* ranged from 7.5 g to 31.5 g, with the majority of individuals weighing between 10.5 g and 13.5 g. Although most individuals clustered within a relatively narrow size range, the presence of a few larger specimens suggests variation in growth stages. The length-frequency distribution showed a moderately skewed unimodal pattern, with fish sizes concentrated between 8.5 cm and 10.5 cm, peaking at 9.5 cm TL. Meanwhile, *A. maculatus* exhibited a relatively broad and normally distributed size range compared to other dominant species in this study. The weight-frequency distribution was slightly right-skewed, with most individuals weighing 200-400 g and a peak at approximately 300 g. Length-frequency analysis showed individuals ranging from 16.5 cm to 36.5 cm TL, with a distinct modal peak between 25.5 cm and 27.5 cm TL.

Table 3. Fish species recorded from three sampling sites: Kuala Larut, Kuala Sangga, and Kuala Gula from the Matang Mangrove Forest Reserve (MMFR). N: Total number of individuals recorded; Wt: Average weight (\pm standard deviation); TL: Average total length (\pm standard deviation). NE: Not evaluated; LC: Least concern; NT: Nearly threatened; DD: Data deficiency under IUCN evaluation

Family	Species name	Symbol	IUCN	Kuala Larut			Kuala Sangga			Kuala Gula		
				N	Wt.	TL	N	Wt.	TL	N	Wt.	TL
Ariidae	<i>Arius venosus</i>	AV	NE	13	30.16 (12.89)	14.81 (2.36)	5	59.86 (33.89)	17.36 (3.61)	3	180.7 (146.9)	23.27 (9.69)
	<i>Arius gogora</i>	AG	NT	1	207.1	28	2	120.05 (120.56)	22.7 (9.9)	0		
	<i>Arius leptotacanthus</i>	AL	NE	0			1	79.3	21.9	0		
	<i>Arius maculatus</i>	AM	NE	48	242.57 (59.25)	29.52 (2.26)	134	215.26 (118.5)	26.93 (4.29)	99	179.31 (51.64)	25.48 (2.95)
	<i>Arius oetik</i>	AO	NE	1	54.2	18.7	0			0		
	<i>Cryptarius truncatus</i>	CT	NE	1	352.7	38	4	439.23 (292.72)	34.8 (4.6)	13	105.33 (72.23)	22.91 (5.54)
	<i>Hexanetimachthys sagor</i>	HS	NE	64	479.46 (218.40)	36.24 (6.04)	43	405.11 (293.24)	33.41 (6.1)	2	492 (16.83)	36.35 (1.77)
	<i>Osteogeneiosus militaris</i>	OM	NE	10	280.18 (91.14)	31.51 (2.85)	5	156.7 (103.33)	25.14 (5.02)	0		
	<i>Plicofollis argyropleuron</i>	Pa	NE	1	545.1	40	2	193.1 (45.33)	25.95 (2.19)	0		
	<i>Plicofollis layardi</i>	PL	NE	1	713.1	43	4	740.5 (330.3)	39.5 (6.01)	0		
Bagridae	<i>Mystus wolffii</i>	MW	LC	1	51.2	18.1	0			0		
Butidae	<i>Butis butis</i>	BB	LC	7	15.69 (6.59)	10.94 (1.41)	0			1	12	10.4
Carangidae	<i>Megalaspis cordyla</i>	MC	LC	0			0			1	50.8	17.6
Chanidae	<i>Chanos chanos</i>	CC	LC	1	318.3	35.5	0			0		
Cynoglossidae	<i>Cynoglossus cynoglossus</i>	CCY	LC	0			4	6.45 (1.26)	9.85 (0.49)	0		
	<i>Cynoglossus lingua</i>	CL	LC	0			1	4.5	10.8	0		
Dasyatidae	<i>Brevitrygon walga</i>	BW	NT	1	112.8	41.1	1	233.1	37	2	162 (44.26)	39.15 (8.84)
Dorosomatidae	<i>Escualosa thoracata</i>	ET	LC	58	6.66 (0.94)	8.69 (0.48)	0			1		
	<i>Anodontostoma chacunda</i>	AC	LC	1	5.5	7.6	3	7.37 (1.12)	8.17 (0.58)	65		
Engraulidae	<i>Setipinna melanochir</i>	SM	DD	0			0			1	57.5	19.7
	<i>Stolephorus indicus</i>	SI	LC	0			3	2.37 (0.29)	6.77 (0.61)	0		
	<i>Thryssa hamiltonii</i>	TH	LC	0			4	13.43 (2.66)	12.03 (0.75)	3	30.23 (8.76)	15.47 (1.37)
	<i>Thryssa kammalensis</i>	TK	DD	80	5.98 (0.9)	9.29 (0.57)	554	6.68 (1.2)	9.54 (0.52)	743	7.21 (1.09)	9.81 (0.48)
	<i>Thryssa mystax</i>	TM	LC	10	12.99 (3.76)	12.22 (0.99)	2	17.3 (9.9)	13.45 (2.33)	0		
Gobiidae	<i>Glossogobius aureus</i>	GA	LC	11	51.97 (35.4)	17.41 (3.79)	0			0		
Haemulidae	<i>Pomadasyus kaakan</i>	PK	LC	11	5.45 (0.55)	7.15 (0.33)	33	5.8 (1.02)	6.93 (0.43)	0		
Latidae	<i>Lates calcarifer</i>	LC	LC	1	271.9	24	0			0		
Mugilidae	<i>Paramugil parmatus</i>	PP	LC	272	12.06 (2.79)	9.09 (0.76)	41	12.25 (4.59)	9.03 (0.63)	94	12.69 (4.83)	9.11 (0.58)
	<i>Planiliza subviridis</i>	PS	LC	74	16.19 (6.81)	11.16 (1.75)	20	18.43 (13.46)	11.48 (1.82)	3	14.9 (2.13)	11.07 (0.46)
Plotosidae	<i>Plotosus canius</i>	PC	NE	0			1	408.7	41.3	0		
Polynemidae	<i>Eleutheronema tetradactylum</i>	ET	NE	1	27.1	14.5	4	15.43 (2.85)	12.43 (0.65)	3	248.8 (196.22)	27.93 (10.66)
Pristigasteridae	<i>Ilisha elongata</i>	IE	NE	15	8.96 (3.11)	10.73 (0.99)	14	11.14 (3.23)	11.1 (1.19)	1	17.9	14.1
Scatophagidae	<i>Scatophagus argus</i>	SA	LC	5	100.04 (34.43)	14.88 (1.80)	5	94.06 (31.07)	14.62 (1.93)	18	89.05 (46.81)	12.83 (2.89)
Sciaenidae	<i>Dendrophysa russelii</i>	DR	LC	0			3	8.2 (0.69)	9.13 (0.23)	1	27.2	12.8
	<i>Johnius macrorhynchus</i>	JM	LC	5	24.5 (11.1)	12.6 (2.35)	15	10.47 (4.78)	10.26 (1.21)	17	9.52 (2.14)	10.55 (0.72)
	<i>Johnius weberi</i>	JW	LC	1	9.2	10.4	1	8.3	9.3	8	8.78 (0.82)	9.63 (0.27)
	<i>Nibea soldado</i>	NS	LC	2	260.1 (24.1)	28.15 (1.85)	0			0		
	<i>Pennahia aneus</i>	PA	LC	0			20	23.37 (17.04)	11.68 (3.02)	46	9.18 (4.13)	9.44 (0.94)
	<i>Protonibea diacanthus</i>	PD	NT	0			1	797.9	44.1	1	785.9	43.8

Sphyraenidae	<i>Sphyraena putnamae</i>	SP	NE	0	0			1	517.4	49.3
Trichiuridae	<i>Lepturacanthus savala</i>	LS	NE	0	1	19.1	33	0		
Zenarchopteridae	<i>Zenarchopterus buffonis</i>	ZB	LC	0	0			1	22.1	20.2
Total number of species				28	30			24		
Total number of fish				697	931			1128		

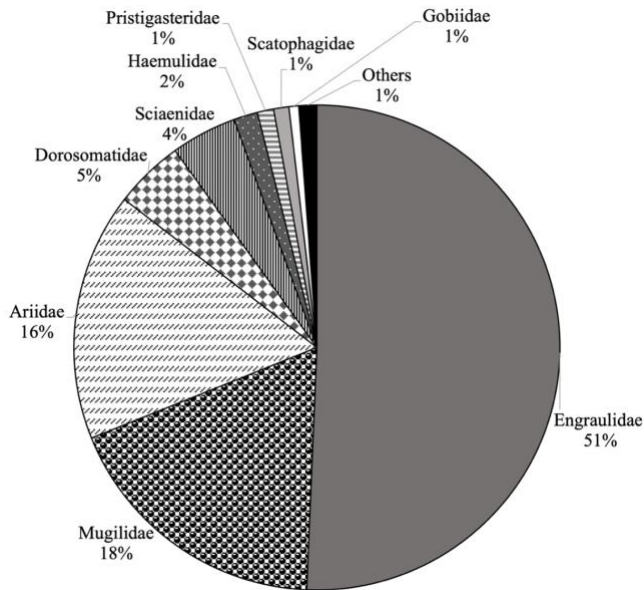


Figure 3. Percentage abundance of estuarine fish families recorded in the MMFR, derived from gill-net samples across all stations. The assemblage was dominated by Engraulidae (51%), followed by Mugilidae (18%) and Ariidae (17%), while other families including Dorosomatidae, Sciaenidae, Haemulidae, Pristigasteridae, Scatophagidae, and 11 additional families, each contributed less than 5% to the total catch

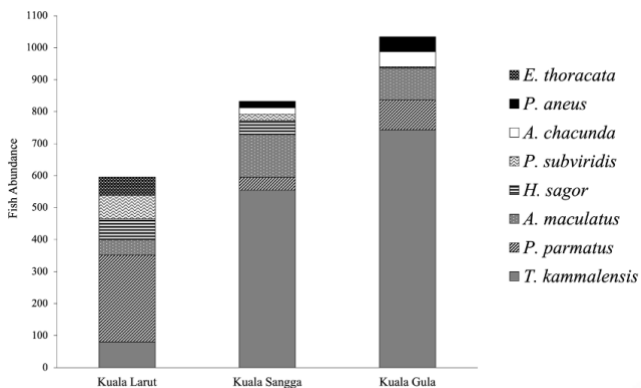


Figure 4. Species-wise distribution of the eight most abundant estuarine fishes recorded in the MMFR. The stacked bars show the total number of individuals captured at each estuary, with shading patterns representing the relative contribution of the dominant species (*Thryssa kammalensis*, *Paramugil parmatus*, *Arius maculatus*, *Hexanemichthys sagor*, *Planiliza subviridis*, *Anodontostoma chacunda*, *Pennahia aneus*, *Escualosa thoracata*) and all remaining species grouped as “others”

Hexanemichthys sagor exhibited a broad and uneven weight-frequency distribution, ranging from 200 g to over 1,800 g. The length-frequency distribution was irregular and multi-modal, with individuals measuring between 28.0 cm and 52.0 cm TL, and several small peaks across this range. Most individuals of *P. subviridis* clustered tightly within a length range of 11.0-12.5 cm TL, peaking at 11.5 cm TL. *A. chacunda* exhibited a moderately spread weight-

frequency distribution, with most individuals weighing 6-9 g and a peak at 7 g. A gradual taper in the distribution was observed towards larger individuals, with the maximum weight recorded at 12 g, suggesting some variation in size classes. The length-frequency distribution ranged from 7.2 cm to 10.0 cm TL, with a prominent peak between 8.0-8.5 cm TL.

Pennahia aneus exhibited a highly right-skewed weight-frequency distribution, with the majority of individuals weighing 5-15 g and a sharp peak at 10 g. Only a few individuals exceeded this range, reaching up to 55 g. The length-frequency distribution mirrored this pattern, with most fish measuring 8.5-10.5 cm TL and peaking at 9.5 cm TL, although occasional larger individuals of up to 15.5 cm TL were recorded. The weight-frequency distribution of *E. thoracata* displayed a multi-modal pattern, with several small peaks between 5 g and 8 g, suggesting an even representation across multiple weight classes and the presence of fish at different growth stages. In contrast, the length-frequency distribution was strongly unimodal, with the majority of individuals measuring 8.5-9.5 cm TL and a clear peak at 9.0 cm TL.

Canonical Correspondence Analysis (CCA)

The global CCA model was statistically significant ($F: 1.894, p: 0.001$), indicating that the measured environmental variables collectively explained a significant proportion of variation in fish community structure. Among the tested environmental variables, depth ($F: 2.182, p: 0.004$), dissolved oxygen ($F: 2.184, p: 0.010$), temperature ($F: 1.933, p: 0.015$), and turbidity ($F: 1.931, p: 0.023$) were found to be significant predictors influencing fish assemblage patterns. In contrast, pH ($p: 0.068$) and salinity ($p: 0.065$) showed marginal effects. Axis-specific permutation tests showed that only the first canonical axis (CCA1) was statistically significant ($p: 0.002$), indicating that it represents the primary gradient structuring fish-environment relationships. Consequently, interpretation of fish assemblage patterns focuses on associations along CCA1 (Figure 7).

The CCA ordination revealed substantial overlap among stations from upper, middle, and front estuary zones, indicating that fish assemblages were not distinctly structured by zonation but rather by continuous environmental gradients, particularly turbidity, depth, temperature, and dissolved oxygen. Although some stations displayed tendencies toward specific environmental drivers (e.g., ST1 towards higher turbidity, ST2 and ST3 towards temperature and dissolved oxygen, and ST6 and ST9 towards salinity and pH), stations did not form distinct clusters corresponding to estuarine zonation. Several stations from different zones (e.g., ST4, ST5, ST7, and ST8) were positioned close to the origin of the ordination, indicating mixed environmental influence and similar fish assemblage composition.

Discussion

Fish assemblages

The absence of clear zonal separation in the ordination likely reflects the dynamic and transitional nature of estuarine systems, where environmental conditions vary gradually rather than abruptly. Processes such as tidal mixing,

freshwater inflow, and sediment resuspension can homogenize environmental conditions across zones, reducing sharp ecological boundaries (Wolowicz et al. 2007; Neves et al. 2011). Consequently, fish species may exhibit broad

environmental tolerances and flexible habitat use, allowing them to occupy multiple zones within the estuary (Loureiro et al. 2016).

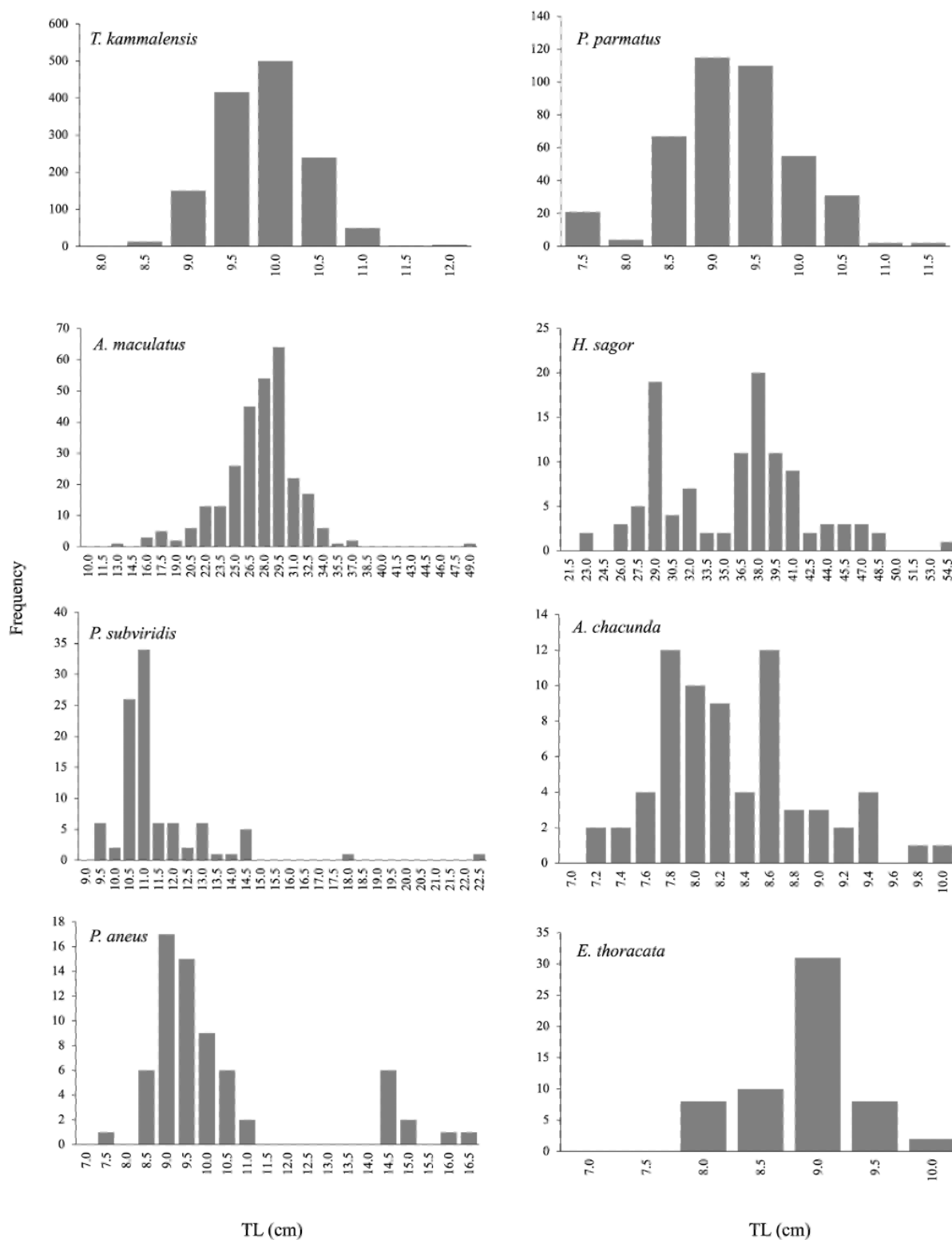


Figure 5. Length-frequency distributions of the eight most abundant fish species in MMFR. *Thyssa kammalensis* (N: 1377), *Paramugil parmatus* (N: 407), *Arius maculatus* (N: 281) and *Hexanematichthys sagor* (N: 109), *Planiliza subviridis* (N: 97), *Anodontostoma chacunda* (N: 69), *Pennahia aneus* (N: 66) and *Escualosa thoracata* (N: 59)

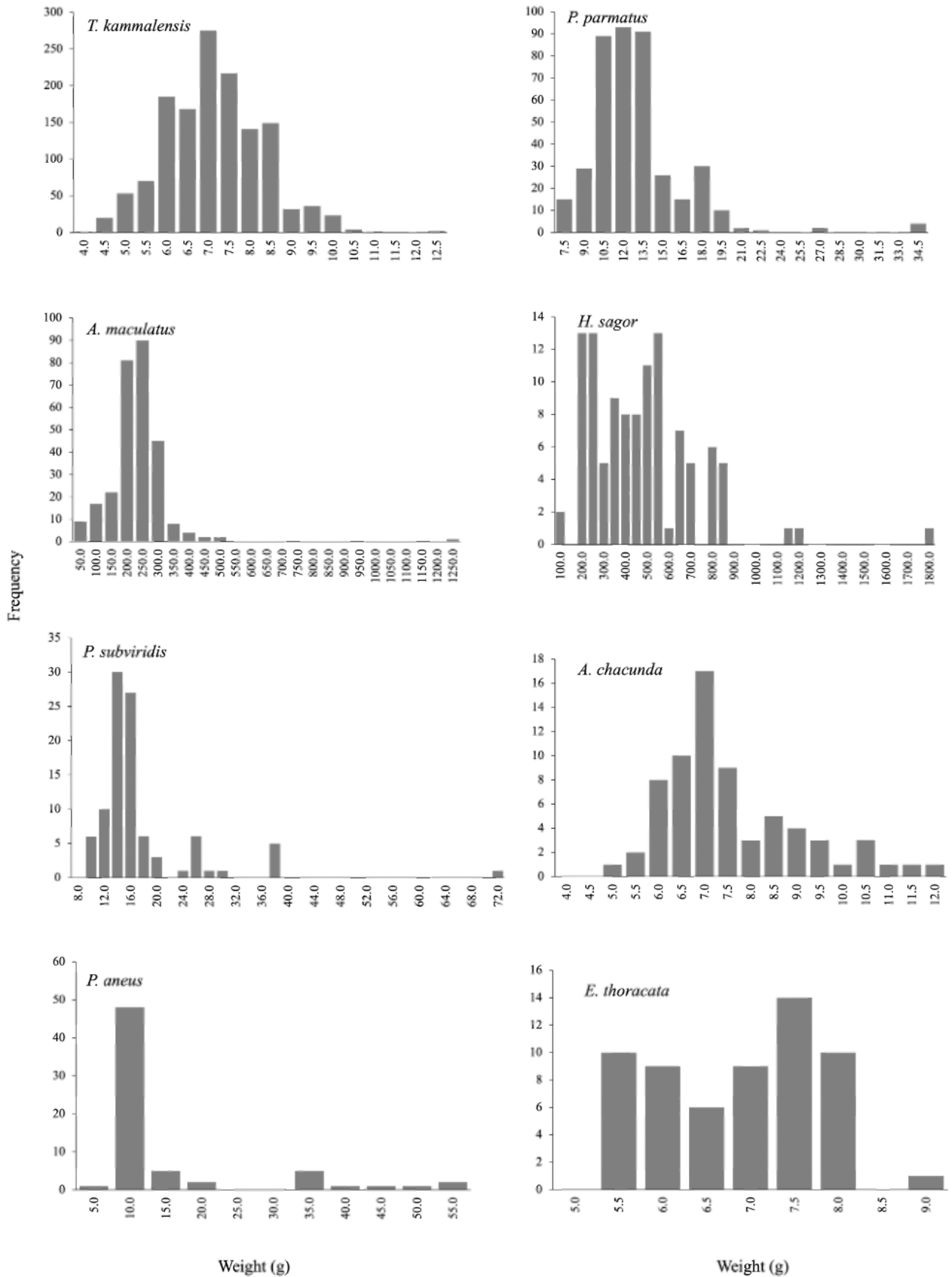


Figure 6. Weight-frequency distributions of the eight most abundant fish species in MMFR: *Thryssa kammalensis* (N: 1377), *Paramugil parmatus* (N: 407), *Arius maculatus* (N: 281) and *Hexanetimacthys sagor* (N: 109), *Planiliza subviridis* (N: 97), *Anodontostoma chacunda* (N: 69), *Pennahia aneus* (N: 66) and *Escualosa thoracata* (N: 59)

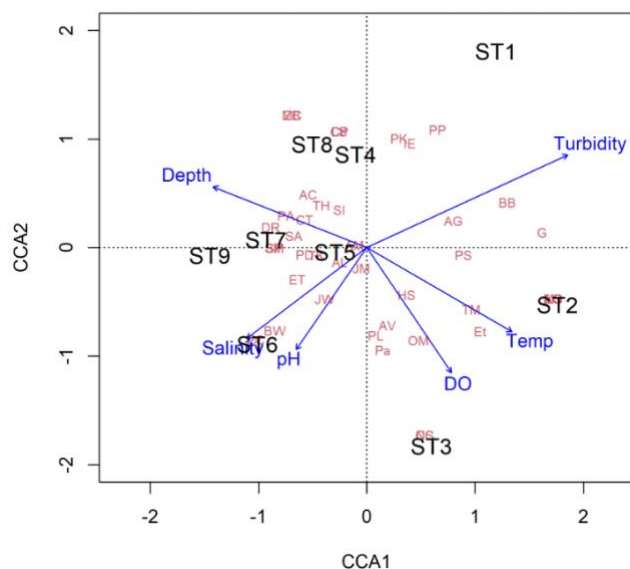


Figure 7. Canonical Correspondence Analysis (CCA) biplots illustrating the relationships between environmental variables (depth, salinity, pH, DO, temperature, and turbidity) and sampling stations (left panel) and fish species composition (right panel). Abbreviation for species is provided in Table 2

Meanwhile, depth, dissolved oxygen, temperature, and turbidity emerged as the main predictors shaping the distribution of fish assemblages within the Matang Mangrove Forest Reserve (MMFR). Previous studies have reported variable and sometimes contrasting associations between environmental variables and estuarine fish assemblages (Pombo et al. 2005; Ram et al. 2025). However, the causal mechanisms underlying these differences are often difficult to fully resolve, largely due to the natural heterogeneity and pronounced temporal and spatial dynamics of estuarine environments.

In general, estuarine fish species are recognized for their high ecological plasticity, allowing them to tolerate wide fluctuations in physicochemical conditions such as salinity, turbidity, and oxygen availability. This adaptability enables many species to occupy multiple zones along the estuarine gradient and likely contributes to the weak zonal segregation observed in the present study. Consequently, fish assemblage structure in MMFR appears to be governed more by continuous environmental gradients and local habitat conditions than by fixed spatial zonation along the estuary.

Smaller fish cohorts

Generally, this study shows that species such as *P. parmatus*, *P. subviridis*, *A. chacunda*, and *P. aneus* were represented by relatively smaller size classes in MMFR compared to published records, particularly those from other regional studies. Compared to regional records, the sizes of *P. parmatus* caught in MMFR are considerably smaller than the maximum size of approximately 30 cm TL reported by Froese and Pauly (2020). In the Bay of Bengal, Rahman et al. (2021) recorded a TL range of 21-39 cm, establishing a new maximum size for the species relative to

earlier reports. In contrast, the size range of 7.5-11.5 cm TL observed in the present study clearly indicates dominance of smaller cohorts, suggesting that the sampled population is dominated by younger age classes.

Meanwhile, both length and weight distributions of *P. subviridis* exhibited a unimodal pattern with a positively skewed trend, indicative of a single dominant cohort with several individuals extending into larger size classes. When compared to other studies, this size range falls into the range is broadly consistent with size classes reported from Makassar Straits by Rahmadhani et al. (2023), where they caught male specimens of *P. subviridis* measured 11.2-29.8 cm in TL and weighed 21.15-233.34 g, whereas females ranged from 11.5-28.0 cm with body weights of 20.09-221.39 g. In a broader sample spanning southern Bangladesh, lengths of *P. subviridis* ranged from 6.5 cm to 19.7 cm TL (Islam et al. 2023), which overlaps with the size range reported in this study. Meanwhile, the size at first maturity reported from Cengklok coastal waters, Banten Bay Indonesia was 13.78 cm for males and 16.39 cm for females (Fitriah et al. 2021) considerably larger than the majority of individuals sampled from MMFR. These differences suggest that the sampled population in this study was composed mainly of a younger cohort.

Previous studies from the Bay of Bengal reported a much larger *A. chacunda*, with TL ranging from 12.50 to 26.70 cm and size at sexual maturity between 15.40 and 16.80 cm TL (Hasan et al. 2024). Similarly, Salim et al. (2024) documented larger populations in North Kalimantan, Indonesia, with males measuring 10.0-15.9 cm TL (12.5-53 g TW) and females 8.0-14.5 cm TL (16.3-60 g TW). In the Patuakhali coastal artisanal fishery survey, Siddik et al. (2016) also recorded larger individuals, ranging from 10.6 to 19.9 cm TL and 15.2 to 91.1 g TW. By comparison, the individuals sampled in this study were considerably smaller, indicating that the population was predominantly composed of juveniles and subadults. This size composition likely reflects seasonal recruitment events and emphasizes the role of estuarine habitats as critical nursery grounds for *A. chacunda*.

The length-frequency distribution of *P. aneus* exhibited a clear bimodal pattern, indicating the coexistence of at least two cohorts within the sampled population, one dominated by recently recruited juveniles and another comprising older subadults, based on the size range smaller and larger to the minimum commercial size often cited for the species (13 cm, TL) as reported by Sivadas et al. (2017). Assessment of the population from Tangerang waters, Indonesia also recorded much larger sizes (Mean 18.9 cm FL), as reported by Wagiyo and Chodriyah (2020) and from northern South China Sea (Mean 18.34 FL) by Tuuli et al. (2011).

Mix and larger fish cohorts

Meanwhile, other dominant species caught in this study were represented by either a mixed size classes, or larger size classes in MMFR compared to the other records. For example, the length of *T. kammalensis* collected from MMFR in this study was considerably smaller than the species' reported maximum of 18.0 cm TL and maximum

published weight of 36.5 g from the coastal waters of Gwangyang Bay, South Korea (Yu et al. 2021) although still larger than than the size of maturing gonad (6.2 cm SL) reported by Sarpéadonti and Ching (2000) from the Sungai Selangor estuary, Malaysia.

The unimodal size distribution pattern of *A. maculatus*, with the exception of a single large individual, suggests that the catch was dominated by a single cohort. The reported length at first maturity for this species is 12.80 cm for males and 11.79 cm for females (Vo et al. 2024), indicating that most individuals sampled in this study were adults. Although *A. maculatus* can reach up to 80 cm TL, the species is more commonly recorded at around 30 cm TL (Froese and Pauly 2024). Previous studies have documented slightly smaller maximum sizes: 23.8 cm TL in Songkhla Lake, Thailand (Phaeviset et al. 2021), 23.7 cm TL in the Mekong Delta (Kutsyn et al. 2021), and 29 cm TL in the Sungai Pulai seagrass beds, all of which are marginally lower than the largest individual observed in the present study. Notably, Phaeviset et al. (2021) also observed that populations inhabiting freshwater and brackish habitats are generally smaller than conspecifics from marine environments, supporting the trends observed here.

On the other hand, the absence of a single dominant size or weight class of another Ariid fish, *H. sagor* suggests the presence of multiple size groups, possibly reflecting species-specific movement patterns, recruitment variability, or the use of different estuarine microhabitats. Both peak size cohorts caught in this study are beyond the length at first sexual maturity for *H. sagor* (25.39 cm) as reported by Huynh et al. (2019). The wide size range observed here therefore likely represents a mixed population containing both reproductively mature adults and older individuals. Such diversity in size structure aligns with observations from other marine catfish populations, which typically contain multiple year classes (Flinn et al. 2019).

Assessment of *E. thoracata* populations from Versova, Bombay recorded a size range of 4.1-10.5 cm TL, with females attaining maturity at 8.2 cm TL (Raje et al. 1994). In the estuarine fisheries of Bangladesh, population dynamics analysis showed that 50% of individuals were harvested at 6.26 cm TL, with an optimum harvestable length estimated at 7.20 cm TL (Rashed-Un-Nabi et al. 2009). Meanwhile, a sustainability assessment from the central west coast of India indicated signs of overfishing, with most of the catch occurring between 8.8-10.1 cm TL, peaking at 9.8 cm, and a maximum recorded length of 11.0 cm TL (Gurjar et al. 2021). The observed size range of 8-10 cm in the present study therefore suggests that the majority of individuals fall within or above the size at first maturity, indicating dominance of potentially mature cohorts in the sampled population.

Ecological and fisheries implications

The prevalence of small-sized individuals and narrow unimodal distributions in *P. parmatius*, *P. subviridis*, *A. chacunda*, and *P. aneus* underscores the role of MMFR as a primary nursery ground for early life stages of clupeids, mugilids, and sciaenids. Estuarine attributes such as sheltered

embayment, reduced predation, and high detrital and planktonic productivity create favorable conditions for recruitment and growth (Elliott and Quintino 2007; Sheaves 2009). The dominance of juvenile cohorts suggests recruitment pulses presumably linked to seasonal spawning cycles, with species such as *T. kammalensis* and *P. subviridis* being strongly estuary-dependent during development, while *P. aneus* shows recruitment peaks tied to coastal spawning events (Azim et al. 2021). These nursery functions are ecologically and economically significant, as they underpin artisanal and small-scale fisheries that depend heavily on sustained juvenile recruitment (Blaber 2000; Chong 2007). However, the reliance of these taxa on estuarine residence makes them highly vulnerable to habitat degradation, hydrological change, and water quality decline, with potential consequences for both biodiversity and local fishery yields. Importantly, the unimodal distributions captured in this study provide a temporal snapshot of recruitment rather than evidence of permanent estuarine residency, reinforcing MMFR's role as a life-stage-specific habitat that supports population replenishment before adults migrate to adjacent coastal waters (Nagelkerken et al. 2008; Sheaves 2009).

In contrast, *T. kammalensis*, *A. maculatus*, *H. sagor*, and *E. thoracata* exhibited broader or multimodal length-frequency distributions, reflecting the presence of multiple cohorts and suggesting that MMFR supports more than just early life stages. The coexistence of juveniles, subadults, and mature individuals indicates that these species use MMFR estuaries as long-term habitats for feeding, growth, and reproduction, thereby highlighting the system's role as a multi-cohort refuge rather than solely a transitional nursery (Blaber 2000; Nagelkerken et al. 2008). For instance, ariid catfishes function as benthic meso-predators, coupling benthic and pelagic energy pathways through diverse diets of fishes, crustaceans, and detritus (Maitra et al. 2020), while *E. thoracata* act as omnivores, capitalizing on the high detrital production typical of mangrove estuaries (Gurjar et al. 2017). The persistence of multiple size classes within MMFR implies continuous habitat use and energy transfer, thereby sustaining trophic dynamics and contributing directly to local fishery catches. From a conservation perspective, these species exemplify the importance of maintaining estuarine integrity not only for recruitment but also for long-term population support. Protecting such multi-cohort assemblages is crucial for ensuring ecosystem resilience, as their ecological roles encompass both resource recycling and stabilizing fishery productivity under environmental variability (Elliott and Quintino 2007; Sheaves 2009).

Conservation value for the near threatened species

The MMFR estuaries represent a productive and ecologically diverse estuarine-mangrove system, underscoring its high conservation importance through the documented occurrence of multiple fish species categorized as Near Threatened (NT) by the IUCN Red List. These species include the black jewfish (*Protonibea diacanthus*), dwarf whipray (*Brevitrygon walga*), and Gagora catfish (*Arius*

gagora), all of which were recorded during field sampling in this study.

The black jewfish (*P. diacanthus*), a member of the Sciaenidae family, inhabits estuarine and coastal waters with muddy substrates and is known to extend offshore to depths of up to 100 m. This large-bodied species feeds opportunistically on crustaceans and small fish and is often targeted due to its high commercial value. Sciaenids are ecologically significant and widely distributed across tropical and subtropical waters, where they typically dominate epibenthic fish communities and serve as a cornerstone for commercial, recreational, and indigenous fisheries (Semmens et al. 2010; Dutta et al. 2014). In MMFR, only two individuals of *P. diacanthus* were recorded, one from KS and another from KG, highlighting the rarity and potential vulnerability of this species in the estuary, consistent with concerns over its overexploitation.

Another Near Threatened species recorded is the dwarf whipray (*B. walga*), which is commercially important in regional fisheries, particularly in Karachi, with larger individuals commonly exported to Thailand and Malaysia. In Malaysia, *B. walga* is typically harvested as bycatch from trawling and gillnet operations and utilized as a food source. Its occurrence is seasonal, peaking between May and October. The incidental capture of this species in the MMFR signals its ecological presence and also the conservation challenges posed by unsustainable fishing practices. The Gagora catfish (*A. gagora*), from the Ariidae family, is known to inhabit estuarine and coastal waters in Bangladesh, Singapore and Malaysia (Ng 2012; Rahman et al. 2020). It has long been considered a valuable food fish, yet its population has faced significant declines over the past two decades due to intense fishing pressure. As a result, the species is now classified as Near Threatened by the IUCN. Its detection in the MMFR further reinforces the area's importance as a habitat for species of conservation concern.

The presence of these Near Threatened species, though in low abundance, strongly underscores the ecological sensitivity and conservation significance of the MMFR. This highlights the urgent need for effective management and monitoring strategies to protect vulnerable species and sustain the biodiversity within this nationally important mangrove and estuarine ecosystem.

In conclusion, the findings of this study demonstrate that fish assemblage structure in the MMFR is shaped primarily by continuous environmental gradients rather than by distinct estuarine zonation, reflecting the highly dynamic and transitional nature of the system. The dominance of small-sized and unimodal cohorts in several key species highlights the critical nursery function of MMFR for early life stages, while the presence of mixed and multi-cohort size structures in other taxa indicates sustained habitat use for feeding, growth, and reproduction. Together, these patterns underscore the dual role of MMFR as both a recruitment hotspot and a long-term refuge that supports trophic connectivity and fisheries productivity. Importantly, the occurrence of Near Threatened species, albeit in low abundance, further emphasizes the high conservation value of this estuarine-mangrove complex and

its vulnerability to environmental degradation and fishing pressure. Protecting the ecological integrity of MMFR is therefore essential not only for maintaining fish biodiversity and population replenishment but also for sustaining the ecosystem services and fisheries that depend on this nationally significant mangrove system.

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