Spatial and Temporal Variation in Abundance and Biomass of Different Sex Classes of the Estuary Prawn *Macrobrachium equidens* (Dana, 1852) (Decapoda, Palaemonidae) From the Mekong Estuaries, With Notes on Its Salinity Tolerance

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E-ISSN: 2073-3720
https://doi.org/10.33997/j.afs.2025.38.3.002

Abstract

The estuarine prawn *Macrobrachium equidens* is among the most frequently exploited fishery resources in the Mekong estuaries, primarily harvested by artisanal fisheries to supply local markets. Despite its ecological and economic importance, the reproductive biology of the species remains poorly understood. This study aimed to investigate the spatio-temporal variation in the abundance and biomass of different sex classes of *M. equidens* across four Mekong estuaries in Southern Vietnam. Samples were collected using a beam trawl at four estuarine locations (Cua Dai, Ham Luong, Ba Lai, and Co Chien) over four sampling periods from March to November 2022. The findings revealed minimal seasonal and spatial variation in the total abundance and biomass of male and female *M. equidens*. However, significant fluctuations were observed in the proportions of non-ovigerous females (%NOF) and ovigerous females (%OF). Spearman analysis showed a positive correlation between %NOF and salinity, while %OF showed a negative correlation with salinity, suggesting that salinity played a key role in regulating the proportions of non-ovigerous and ovigerous females of *M. equidens* in Mekong estuaries. The study also showed that the period of highest production of *M. equidens* in the Mekong estuaries appears to coincide with the peak of the rainy season, from August to November. This research provides important insights into the reproductive biology of estuarine prawn, enhancing our understanding of their adaptive approaches and reproductive capabilities in relation to environmental conditions.

Keywords: benthic fauna, crustaceans, fisheries, Mekong Delta, salinity intrusion

Introduction

Decapod crustaceans are a vital food source for both humans and animals, playing a significant role in the aquaculture industry by contributing to food production and generating income for many countries (Reantaso et al., 2012). Vietnam is home to approximately 41 species of freshwater shrimp, classified into two families: Atyidae and Palaemonidae (Thanh and Hai, 2012). Among these, the Palaemonidae family is particularly noteworthy due to its high nutritional and economic value (Thanh and Hai, 2001). The genus *Macrobrachium* within the Palaemonidae family, comprises approximately 240 species (Wowor et al., 2009), many of which possess significant economic potential and abundant stocks (Ibim, 2018). This genus is widespread in tropical and subtropical freshwater and brackish water environments globally (Short, 2004), largely due to its highly adaptable reproductive and life history strategies (Short, 2004; Pileggi and Mantelatto, 2010). In Vietnam, 18 species of *Macrobrachium* have been recorded, inhabiting both freshwater environments and coastal areas (Thanh and Hai, 2001; Nguyen and Truong, 2004). Notable species in the Vietnamese Mekong Delta include *M. rosenbergii*, *M. mirabile*, *M. esculentum*, *M. javanicum*, *M. sintangense*, *M. equidens*, *M. mamillodactylus*, *M. lanchesteri*, and *M. idea* (Nguyen and Truong, 2004). Of these, the giant freshwater prawn (*M. rosenbergii*) is of the highest economic value, while other species, such as *M. equidens* (Dana, 1852), are abundant and serve as a crucial daily food source for local populations,

underscoring their significance as a resource for local fishermen (Thanh and Hai, 2001).

The freshwater prawn species within the *Macrobrachium* genus are commonly found and plentiful in various aquatic environments (Cook et al., 2002). Consistent with this, *M. equidens* is widely distributed across tropical and subtropical regions globally (Maciel et al., 2011). This species inhabits a variety of environments, ranging from freshwater bodies to estuaries and coastal mangrove forests (Ghory et al., 2022), and it is even capable of thriving in polluted waters (Short, 2004). Although native to the Indo-Pacific region, *M. equidens* has now become an invasive species in Brazil (Maciel et al., 2011) and West Africa (Powell, 1986). Despite its economic and nutritional importance, scientific knowledge on the biology, ecology, and spatio-temporal distribution of *M. equidens* in the Mekong River estuary and the broader Mekong Delta remains limited.

Prawn communities within an ecosystem are influenced and shaped by a complex interplay of biotic and abiotic factors, which together create discernible biotic patterns (González-Ortegón et al., 2023). In temperate estuaries, temperature is a key determinant of breeding periods, growth rates, reproductive success, and temporal fluctuations in both abundance and biomass (Szedlmayer and Able, 1996). Conversely, in tropical estuaries, salinity predominantly governs the spatiotemporal distribution of decapod crustaceans (Benchamin et al., 2024). Changes in salinity, particularly those caused by the holding back freshwater flow from rivers into estuaries, can significantly impact water quality and lead to "unexpected" reductions in salinity during both dry and rainy seasons, thereby affecting the structure and interactions of decapod populations in estuarine habitats (Fernández-Delgado et al., 2007). However, there has been limited research on how prawn communities in the Mekong Delta respond to varying salinity conditions. Ikejimba and Sakpa (2014) further emphasised that any environmental changes could disrupt the sustainability and threaten the biodiversity of prawn communities. For instance, rising temperatures may result in decreased dissolved oxygen levels, which could reduce the abundance of species such as *M. felicinium* and *M. lux* (Topuz and Kır, 2023). Additionally, water depth significantly influences the abundance of certain *Macrobrachium* species, with deeper waters negatively correlated with the abundance of *M. macrobrachion, M. vollenhovenii, M. felicinium*, and *M. lux* (Omoregie, 2016). Nutrient levels (nitrate, phosphate, sulphate) have also been positively correlated with the number of individuals of *M. vollenhovenii, M. lux*, and *M. felicinium* (Omoregie, 2016).

While these insights into environmental factors affecting *Macrobrachium* species are valuable for aquaculture, most studies on freshwater prawn have predominantly focused on taxonomy (Eniade and Olusoji, 2011). In Vietnam, research on prawn fauna has largely been centred around taxonomy (Nguyen, 2006; Marin, 2008; Ďuris et al., 2008; Tu and Cuong, 2014), resources (Tu and Pham, 2014; Tu et al., 2023), bioaccumulation (Tu et al., 2008), molecular biology (Hung et al., 2013), and aquaculture (Thanh et al., 2009). However, there have been limited studies exploring the interactions between prawn communities and environmental conditions. Understanding this ecological relationship is crucial for effective fishery management (Kritzer, 2004).

Estuaries are a critical component of the Mekong River ecosystem, supporting the highest levels of aquatic biodiversity within the river system due to the confluence of freshwater, brackish, and marine organisms (Jorgensen and Visser, 2002). These estuaries also serve as reservoirs for sediments and organic matter from the Mekong River system, enriching the region with nutrients that drive its high biological productivity (Grimes and Finucane, 1991). As a result, the fishing industry, particularly prawn and fish harvesting, is highly developed and serves as the primary source of income for local communities (Campbell, 2009). Although there is extensive scientific data on the biodiversity of fish communities in the Mekong estuary (Tran et al., 2013), other aquatic groups have been less thoroughly studied. Some preliminary research has been conducted on specific aquatic groups, such as free-living nematodes (Ngo et al., 2016; Nguyen et al., 2020; Tran et al., 2022), large benthic invertebrates (Tran et al., 2020), and phytoplankton (Tran Yen et al., 2022) within the Mekong estuaries. However, scientific data on prawn communities-a group of considerable economic importance remains limited.

Given the potential significance of *M. equidens* for a vital fishery in the Mekong estuaries, acquiring biological data on fisheries such as spatio-temporal distribution and ecological relationships is crucial for effective fisheries management (Shin et al., 2005). This knowledge facilitates the development and execution of management strategies, such as protected breeding areas and fishing bans, which promote sustainable use, alongside monitoring and conservation approaches (Aragón-Noriega and García-Juárez, 2007). Against this backdrop and considering the limited research on the spatial and temporal dynamics of *M. equidens* in the Mekong estuaries, the primary objective of this study was to assess spatial and temporal variation in the abundance and biomass of different sex classes of the estuarine prawn *M. equidens* in the Mekong estuaries, with additional observations on its salinity tolerance.

Materials and Methods

Ethical approval

Fieldwork and sample processing adhere to applicable regulations, with a focus on minimising pain and distress to study animals. Sample sizes are limited but sufficient to meet research objectives, while also taking into account

the conservation status of the target species. Destructive or invasive techniques are employed sparingly. Since the research involved an unregulated invertebrate species, no ethics committee approval was required.

Area of investigation

The Mekong River, upon entering Vietnam, splits into two main branches: the Hau River (Bassac) and the Tien River. These branches form the Mekong Delta. The Hau River further divides into the Tran De and Dinh An branches near the sea. The Tien River splits into the Co Chien and My Tho branches at Vinh Long. The Co Chien branch later divides into the Co Chien and Cung Hau estuaries, while the My Tho branch splits into the Cua Dai, Cua Tieu, Ba Lai, and Ham Luong estuaries, creating a complex network of waterways in the delta.

It has a tropical monsoon climate, characterised by high temperatures (average of 28 °C), small thermal range and abundant rainfall with 1,500–2,500 mm annually. The months of highest rainfall are July to December, when the rain is intensive in the region (Le et al., 2006).

This area is rich in aquatic environments, encompassing dense water bodies such as coastal lagoons and mangrove ecosystems, which are critical as nursery habitats and designated zones for prawn larvae. In addition, a network of spider-like riverine channels converges in this region, transporting nutrients that significantly enhance biological productivity and contribute to the formation of estuarine complexes vital for prawn nursing (Truong and Do, 2018).

Sampling and sample treatment

While the Mekong estuary includes more branches, this study focuses specifically on four: Cua Dai (CD), Ba Lai (BL), Ham Luong (HL), and Co Chien (CC) (Fig. 1).

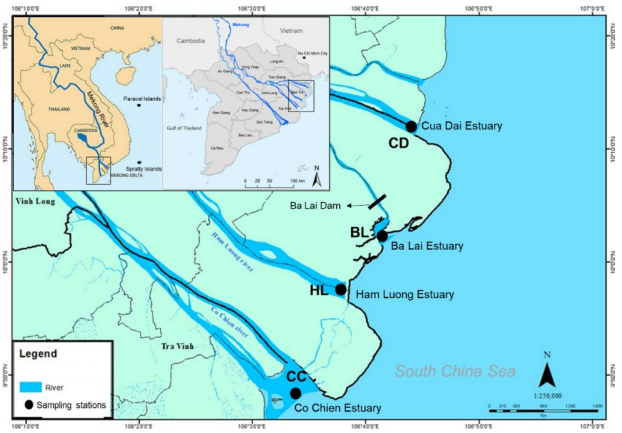

Fig. 1. Map of the Mekong estuaries (Southern Vietnam), indicating the locations of four sampling sites (●) between March and November 2022.

Prawn were sampled four times between March and November 2022 using a 4-metre beam trawl with 20 mm mesh size. To facilitate comparisons with previously published data, prawn abundance was standardised and expressed as individuals per 1,000 square meters (inds.1000 m^{-2}) (de Carvalho et al., 2016). The sampled area was calculated by multiplying the trawl beam width (m) by the trawling distance (m), which was accurately measured using a Garmin GPSMAP 76CSx (Taiwan). After collection, the prawn were promptly frozen and transported to the laboratory for further analysis. In the lab, the samples were pre-sorted, and the organisms were preserved in 96 % ethanol for later identification. The species *M. equidens* was separated from the overall sample, with its numbers and wet weights recorded. Post-identification, these prawn were weighed, and all wet weights were adjusted by a factor of 1.2 to account for weight changes due to ethanol preservation (Zintzen et al., 2008a, 2008b). Individuals were sexed through visual examination of the second pereopods, following the method described by Powell (1982). To confirm male identity, the presence of the appendix masculina on the second pereopods was used as a distinguishing characteristic, as noted by Edokpayi (1990) (Fig. 2).

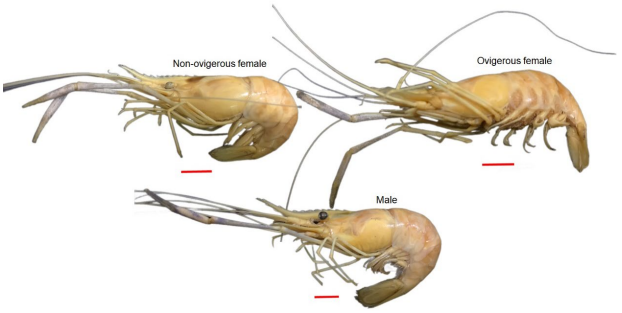

Fig. 2. The estuary prawn *Macrobrachium equidens* (Dana, 1852) in different sex classes. Scale bar: 1 cm.

The seasons were categorised into dry and rainy periods, with sampling conducted in March and June for the dry season, and in August and November for the rainy season, each with two replicates. Overlying water samples were taken for physical and chemical properties. Salinity, temperature, pH, and dissolved oxygen (DO) were recorded on-site using a multiparameter water quality meter (WQC-22A, DKK-TOA, Japan). Total suspended solids (TSS) were quantified in accordance with the SMEWW 2540 method. All procedures adhered to internationally recognised sampling protocols as outlined in ISO 5667-1:2006 and ISO 5667-3:2018 standards. Water depth measurements were conducted utilising a time-depth recorder (TDR 1100, Lotek, Canada).

Data analysis

The adult sex ratio (ASR) was calculated as the number of males divided by the total number of males and females (Ancona et al., 2017). This measure is symmetric around 0.5 and ranges from 0 (indicating an all-female population) to 1 (indicating an all-male population). Therefore, it allows for an equal potential

bias toward both sexes on the same scale. We calculated ASR for the species per estuary (CD, BL, HL, and CC) and per season (dry and rainy).

Significant differences in the abundance and biomass of various sex classes of *M. equidens* across estuaries and seasons were assessed using a two-factor ANOVA. The factors included estuaries (Es: Co Chien, Ham Luong, Ba Lai, and Cua Dai) and seasons (Se: Dry and rainy), along with a fixed interaction term for estuaries and seasons. The analysis was conducted using Statgraphics 18. Prior to conducting the ANOVA, data were square root-transformed. The same analytical approach was applied to assess spatial and temporal variations in environmental variables.

Redundancy analysis (RDA) was conducted to examine the multivariate relationships between the abundance and biomass of various sex classes of *M. equidens* and environmental predictors. Monte Carlo permutation tests were employed to further refine the environmental variables, retaining only those significantly correlated with the derived axes. Redundancy analysis and ordination plotting were performed using CANOCO version 4.5 for Windows. Furthermore, non-parametric Spearman rank correlation coefficients ($P < 0.05$) were calculated to identify associations between environmental variables and prawn characteristics. Analysis of variance and correlation tests were conducted using Statgraphics 18.

Results

Environmental factors

All data on environmental variables are shown in Figure 3. Salinity tended to decrease from the dry season to the rainy season. This pattern was most pronounced at the Co Chien and Ham Luong estuaries, where salinity reached its peak during the dry season, with values of 10.91 ± 8.10 PSU and 10.24 ± 8.06 PSU, respectively, before declining to the lowest levels in the rainy season at 0.28 ± 0.32 PSU and 1.94 ± 2.16 PSU, respectively. Similarly, at the Ba Lai and Cua Dai estuaries, salinity declined from 14.30 ± 6.81 PSU and 11.16 ± 9.20 PSU during the dry season to 5.59 ± 2.98 PSU and 5.32 ± 5.27 PSU, respectively, in the rainy season. The two-way ANOVA results revealed significant differences in water salinity across estuaries (P_{Es} = 0.0165) and seasons ($P_{Se} < 0.0001$). Pairwise comparisons showed a significant spatial effect only at the Co Chien and Ba Lai estuaries (CC < BL; Table 1).

The pH levels were slightly alkaline, ranging from 7.21 ± 0.21 at the Ba Lai estuary during the rainy season to 7.63 ± 0.11 at the Co Chien estuary during the dry season. At all four estuaries, pH values were higher in the dry season compared to the rainy season; however, two-way ANOVA results indicated no significant differences with respect to estuaries, seasons, or their interaction (estuaries × seasons). Likewise, temperature was generally higher during the dry season compared to the rainy season, with values ranging from 29.19 ± 0.91 °C at the Ham Luong estuary in the rainy season to 30.63 ± 0.86 °C at the Cua Dai estuary in the dry season. No statistically significant differences in temperature were detected for the factors - estuaries, seasons, or their interaction (Table 1).

Dissolved oxygen (DO) levels were notably low at the Co Chien and Ham Luong estuaries during the rainy season, with values of 3.84 ± 0.43 mg.L^{-1} and 3.64 ± 1.20 mg.L^{-1}, respectively. In other estuaries, DO ranged from 4.90 ± 0.57 mg.L^{-1} at the Ba Lai estuary in the rainy season to 5.71 ± 0.91 mg.L^{-1} at the Cua Dai estuary in the dry season. Statistically significant differences were found among estuaries (P_{Es} = 0.028), seasons (P_{Se} = 0.0003), as well as the interaction estuaries × seasons ($P_{Es×Se}$ = 0.041). Post hoc comparisons revealed distinctions between the Cua Dai estuary and the Co Chien, Ham Luong estuaries (CC < CD, HL < CD; Table 1).

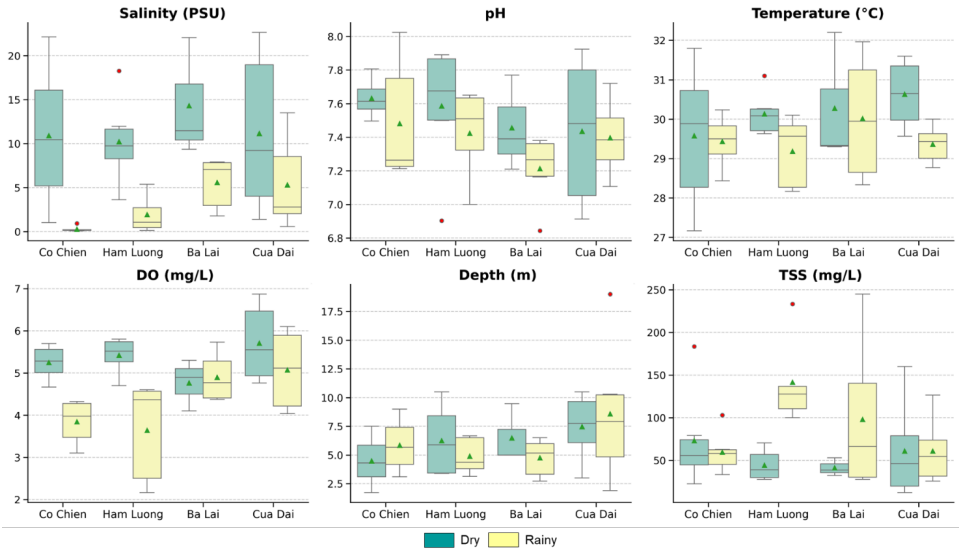

Fig. 3. Abiotic factors were recorded at four Mekong estuaries during both the dry and rainy seasons, spanning the period from March to November 2022.

Table 1. Analysis of variance (ANOVA) summary, testing for differences in the environmental factors between estuaries (Es: Co Chien CC, Ham Luong HL, Ba Lai BL, and Cua Dai CD), seasons (Se: Dry, rainy).

Variables	Factors	*P*	Pairwise comparison
Salinity (PSU)	Es	**0.0165**	CC < BL
	Se	**<0.0001**	Rainy < Dry
	Es × Se	0.098	
pH	Es	0.403	
	Se	0.124	
	Es × Se	0.903	
Temperature (°C)	Es	0.559	
	Se	0.070	
	Es × Se	0.599	
DO (mg.L^{-1})	Es	**0.028**	CC < CD, HL < CD
	Se	**0.0003**	Rainy < Dry
	Es × Se	**0.041**	*
Depth (m)	Es	0.202	
	Se	0.796	
	Es × Se	0.572	
TSS (mg.L^{-1})	Es	0.376	
	Se	**0.029**	Dry < Rainy
	Es × Se	0.188	

Bold values denote statistical significance at the $P < 0.05$ level.
*Pairwise comparisons were conducted only for the factors estuaries (Es) and seasons (Se) when their ANOVA *P*-values < 0.05.

Depth varied from 4.49 ± 2.18 m at the Co Chien estuary in the dry season to 8.59 ± 6.04 m at the Cua Dai estuary during the rainy season. Total suspended solids (TSS) concentrations ranged from 41.26 ± 10.57 mg.L^{-1} at the Ba Lai estuary in the dry season to 141.60 ± 53.25 mg.L^{-1} at the Ham Luong estuary in the rainy season. There was a statistically significant seasonal effect on TSS (P_{Se} = 0.029), with no significant differences detected across estuaries or interaction terms (Table 1).

Spatial variations

Spatial variation in the mean abundance and biomass of different sex classes, including non-ovigerous females (NOF), ovigerous females (OF), total females (F), and males (M), is presented in Figure 4. For NOF prawn, the Co Chien estuary recorded the lowest abundance and biomass, with values of 5.75 ± 8.72 inds.1000 m^{-2} and 8.82 ± 12.72 g.1000 m^{-2}, respectively. In contrast, the highest abundance and biomass were observed at the Cua Dai estuary, at 10.83 ± 15.05 inds.1000 m^{-2} and 33.56 ± 57.68 g.1000 m^{-2}. The abundance of NOF prawn was higher at the Ba Lai estuary compared to Ham Luong, although their biomass did not differ significantly between these two sites. A two-way ANOVA confirmed that neither the abundance nor biomass of NOF prawn differed significantly among estuaries (Table 2).

For OF prawn, both abundance and biomass at the Co Chien and Ba Lai estuaries were markedly lower compared to those at Cua Dai and Ham Luong. The lowest values were recorded at Co Chien (7.17 ± 8.76 inds.1000 m^{-2} and 36.80 ± 46.53 g.1000 m^{-2}), whereas the highest were at Cua Dai (26.67 ± 18.63 inds.1000 m^{-2} and 150.82 ± 144.75 g.1000 m^{-2}). Two-way ANOVA revealed significant spatial differences in both abundance and biomass of OF prawn, with Ba Lai and Co Chien differing significantly from Cua Dai (BL < CD, CC < CD).

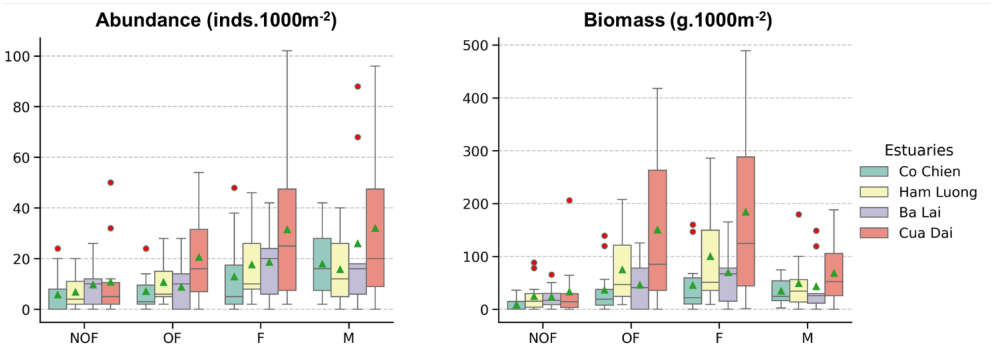

Fig. 4. Means and standard deviations for abundance (number of individuals.1000m^{-2}) and biomass (g.1000m^{-2}) for different sex classes of *Macrobrachium equidens* (non-ovigerous females NOF, ovigerous females OF, total females F, and total males M) at four Mekong estuaries: Co Chien, Ham Luong, Ba Lai, and Cua Dai. Notes: Lines: medians, triangle: means, box: 25th and 75th quartiles, whiskers: the highest and lowest values.

Table 2. Analysis of variance (ANOVA) summary, testing for differences in abundance and biomass for different sex classes of *Macrobrachium equidens* (non-ovigerous females NOF, ovigerous females OF, total females F, and total males M) between estuaries (Es: Co Chien CC, Ham Luong HL, Ba Lai BL, and Cua Dai CD), seasons (Se: Dry, rainy).

Characteristics	Factors	Abundance		Biomass	
		P	Pairwise comparison	*P*	Pairwise comparison
NOF	Es	0.255		0.151	
	Se	**0.002**	Rainy < Dry	**0.009**	Rainy < Dry
	Es × Se	0.304		0.606	
OF	Es	**0.044**	BL < CD, CC < CD	**0.021**	BL < CD, CC < CD
	Se	0.754		0.792	
	Es × Se	0.119		0.158	
F	Es	0.133		0.050	
	Se	0.178		0.290	
	Es × Se	0.302		0.416	
M	Es	0.514		0.397	
	Se	0.870		0.847	
	Es × Se	0.134		0.193	
%NOF	Es	**0.021**	CC < BL	**0.013**	CC < BL
	Se	**<0.001**	Rainy < Dry	**<0.0001**	Rainy < Dry
	Es × Se	**0.041**	*	**0.018**	*
%OF	Es	**0.012**	BL < CD, BL < HL	**0.014**	BL < CD, BL < HL
	Se	**0.012**	Dry < Rainy	**0.022**	Dry < Rainy
	Es × Se	0.116		0.125	
Adult sex ratio (ASR)					
	Es	0.185			
	Se	0.233			
	Es × Se	0.741			

Bold values denote statistical significance at the $P < 0.05$ level.
*Pairwise comparisons were conducted only for the factors estuaries (Es) and seasons (Se) when their ANOVA *P*-values < 0.05.

Total abundance of F prawn across estuaries ranged from 12.92 ± 16.11 to 31.50 ± 29.08 inds.1000 m^{-2}, while M prawn ranged from 18.00 ± 13.54 to 32.00 ± 31.50 inds.1000 m^{-2}. The lowest total biomass of both F and M prawn was observed at Co Chien (45.62 ± 54.33 g.1000 m^{-2} and 34.66 ± 26.07 g.1000 m^{-2}, respectively), whereas the highest was recorded at Cua Dai (184.38 ± 176.05 g.1000 m^{-2} for F prawn and 68.79 ± 60.27 g.1000 m^{-2} for M prawn). However, no significant differences were found in the total abundance or biomass of F and M prawn among estuaries (Table 2).

Overall, only the OF shrimp exhibited significant spatial variation in both abundance and biomass. In contrast, the NOF, F, and M prawn of *M. equidens* did not display significant spatial variation, with no detectable differences among estuaries.

The relative proportions of *M. equidens* ovigerous female (OF) prawn abundance ranged from 39.44 % to 70.02 %, with biomass ranging from 50.88 % to 78.50 %. Thus, OF prawn exhibited higher ratios of both abundance and biomass compared to non-ovigerous females (NOF) across most estuaries, except in Ba Lai, where the NOF prawn had higher relative abundance (60.55 %) (Fig. 5). The ratios of abundance and biomass between NOF and OF prawn were found to differ significantly among estuaries. Post-hoc Tukey HSD analysis revealed a significant difference in the relative proportions of NOF prawn only between the Co Chien and Ba Lai estuaries (CC < BL). However, for OF prawn, significant differences were observed between both Co Chien and Ba Lai estuaries and the Cua Dai estuary (BL < CD, CC < CD) (Table 2).

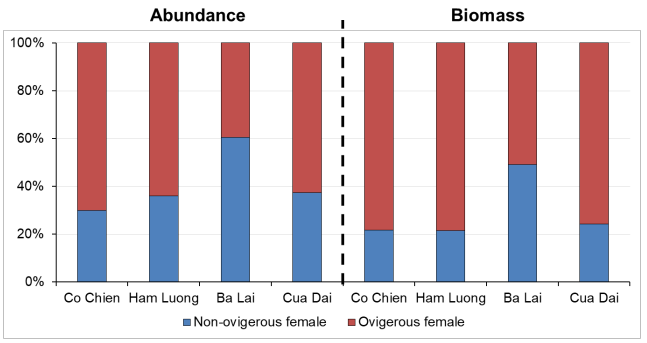

Fig. 5. Spatial variation in the relative ratios of the abundance and biomass of different groups of female of *Macrobrachium equidens* in the four Mekong estuaries.

The ASR value across the estuaries ranged from 0.45 (Cua Dai estuary) to 0.64 (Co Chien estuary). Thus, the Co Chien estuary tended to be male-biased, the ASR at the other estuaries was relatively balanced, indicating an approximately equal proportion of females and males (Fig. 6). The results of the ANOVA analysis

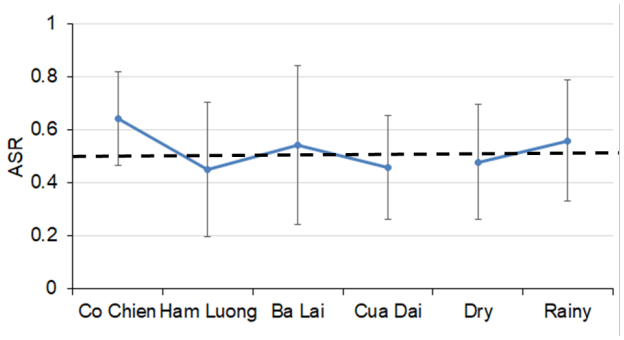

Fig. 6. Spatial and seasonal variation in the adult sex ratio (ASR) of *Macrobrachium equidens*. The dashed horizontal lines at 0.5 indicate the equilibrium ASR, where the number of females and males is equal.

showed no significant differences in the adult sex ratio (ASR) among estuaries (P_{Es} = 0.185), suggesting a lack of spatial variation in this parameter. Accordingly, the total abundance and biomass of both females (F) and males (M), as well as the ASR, did not vary significantly across estuaries. Spatial variation was only detected in the abundance, biomass, and relative proportions (by abundance and biomass) of the female subgroups, namely non-ovigerous females (NOF) and ovigerous females (OF), with the most pronounced differences observed in the ovigerous females.

Seasonal variations

The mean abundance and biomass of different sex classes, including non-ovigerous females (NOF), ovigerous females (OF), total females (F), and males (M), were generally higher in the dry season compared to the rainy season (Fig. 7). The abundance and biomass of NOF prawn were markedly higher during the dry season, with values of 11.29 ± 8.39 inds.1000 m^{-2} and 28.72 ± 24.29 g.1000 m^{-2}, respectively, compared to 5.48 ± 11.45 inds.1000 m^{-2} and 17.13 ± 43.94 g.1000 m^{-2} in the rainy season. Two-way ANOVA confirmed that both the abundance and biomass of NOF prawn differed significantly between seasons (Table 2). In contrast, ANOVA results indicated no significant seasonal differences in the abundance or biomass of OF, F, and M prawn (Table 2), although dry season values remained consistently higher than those in the rainy season. For example, the dry season abundances of OF, F, and M prawn were 12.29 ± 11.35, 23.57 ± 16.51, and 22.57 ± 16.10 inds.1000 m^{-2}, respectively, while those in the rainy season were 11.91 ± 15.13, 17.39 ± 23.82, and 23.22 ± 29.17 inds.1000 m^{-2}. Overall, the abundance and biomass of OF, F, and M prawn of *M. equidens* did not exhibit substantial temporal fluctuations.

While the abundance and biomass of different sex classes of *M. equidens* did not exhibit significant temporal variation, the relative proportions of abundance and biomass among female groups showed notable differences across survey periods (Fig. 8). The relative proportion of NOF prawn in terms of abundance was higher in the dry season (54.85%) compared to the rainy season (24.13 %). In contrast, both the abundance and biomass proportions of ovigerous females (OF) were substantially higher in the rainy season (75.87 % and 83.09 %, respectively) than in the dry season (45.15 % and 61.28 %, respectively). These patterns indicate that NOF prawn were more dominant during the dry season, particularly in terms of abundance, whereas OF prawn were more prevalent during the rainy season, with a clear dominance reflected in both abundance and biomass.

The ASR values during the dry and rainy seasons were 0.48 and 0.56, respectively, indicating a female-biased sex ratio. Indeed, no significant difference in ASR was observed between the dry and rainy seasons (P_{Se} = 0.233) (Fig. 6). Overall, the adult sex ratio showed no significant variation either spatially (among estuaries) or temporally (between seasons).

Relationship between environmental variables and abundance/biomass of each sex class of Macrobrachium equidens

Spearman correlations were calculated between different sex classes of *M. equidens* and environmental variables (Table 3). The relative proportions of abundance (%A.OF) and biomass (%B.OF) for ovigerous females were negatively correlated with salinity. In

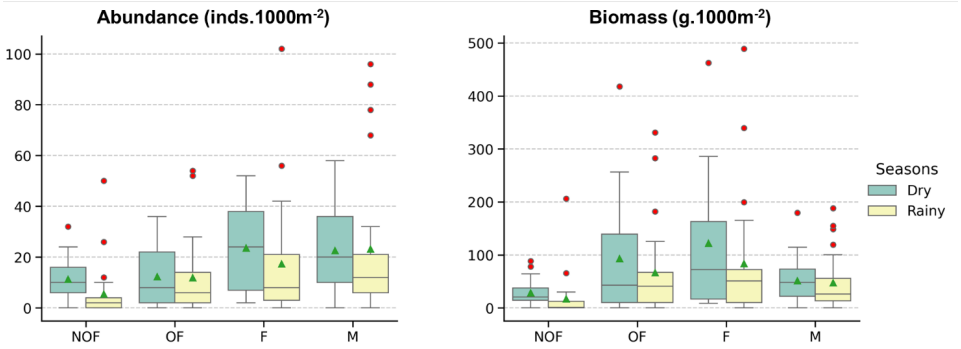

Fig. 7. Means and standard deviations for abundance (number of individuals.1000 m^{-2}) and biomass (g.1000 m^{-2}) for different sex classes of *Macrobrachium equidens* (non-ovigerous females NOF, ovigerous females OF, total females F, and total males M) for the dry and rainy. *Notes:* Lines: medians, triangle: means, box: 25th and 75th quartiles, whiskers: the highest and lowest values.

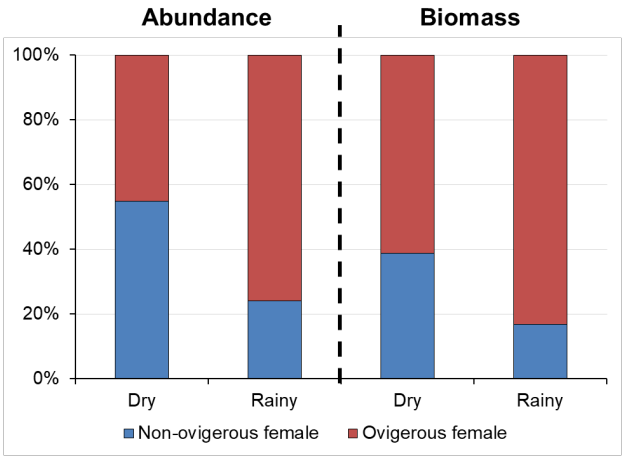

Fig. 8. Seasonal variation in the relative ratios of abundance and biomass for different groups of female of *Macrobrachium equidens*.

Table 3. Spearman correlation coefficients (*r*) between environmental variables and abundance (A)/biomass (B) of each sex class of the estuary prawn *Macrobrachium equidens* (non-ovigerous females NOF, ovigerous females OF, total females F, and total males M).

Characteristics	Salinity (PSU)	pH	Temperature (°C)	DO (mg.L^{-1})	Depth (m)	TSS (mg.L^{-1})
A.NOF	0.43**	0.04	0.18	0.47**	-0.05	-0.21
A.OF	0.07	0.03	0.20	0.33*	0.02	-0.18
A.F	0.28	0.04	0.16	0.44**	0.00	-0.24
A.M	0.13	-0.11	0.13	0.36*	-0.16	-0.11
B.NOF	0.45**	0.11	0.27	0.43**	-0.01	-0.18
B.OF	0.09	0.07	0.19	0.32*	0.04	-0.16
B.F	0.24	0.08	0.17	0.38*	0.02	-0.19
B.M	0.11	-0.08	0.22	0.32*	-0.10	-0.12
%A.NOF	0.57***	0.08	-0.08	0.37*	0.00	-0.14
%A.OF	-0.43**	0.09	-0.02	-0.25	0.12	0.03
%B.NOF	0.54***	0.12	-0.04	0.28	-0.06	-0.06
%B.OF	-0.39*	0.05	-0.05	-0.16	0.18	-0.05
Adult sex ratio (ASR)	-0.24	-0.24	-0.01	-0.15	-0.22	0.10

Significant differences are indicated by asterisk(s): * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

contrast, the abundance (A.NOF) and biomass (B.NOF) of non-ovigerous females, along with their relative abundance (%A.NOF) and biomass (%B.NOF), showed a positive correlation with salinity. In addition, DO exhibited a significant positive correlation with the majority of prawn descriptors, whereas other environmental variables demonstrated no statistically significant relationships.

The decline in salinity from the dry to the rainy season led to an increase in the relative proportions of abundance (%A.OF) and biomass (%B.OF) for ovigerous females, while simultaneously causing a decrease in the relative proportions of abundance (%A.NOF) and biomass (%B.NOF) for non-ovigerous females. The reduction in salinity also resulted in a decrease in the absolute abundance (A.NOF) and biomass (B.NOF) of non-ovigerous females from the dry to the rainy season. In contrast, the abundance (A.OF) and biomass (B.OF) of ovigerous females did not show a correlation with salinity, which may explain their relatively stable seasonal patterns (Table 2).

The redundancy analysis (RDA) demonstrated that physicochemical variables exerted significant spatial and temporal influences on the prawn descriptors (Fig. 9). The first two axes, RDA1 and RDA2, explained 89.90 % of the variability in the relationship between prawn characteristics and environmental factors. Among these variables, salinity and dissolved oxygen (DO) emerged as the most influential factors shaping the traits of *M. equidens*. In terms of spatial distribution, salinity and DO were notably higher at the Cua Dai estuary (Fig. 9A). Temporally, these parameters showed elevated levels in the dry season (Fig. 9B). Given the positive correlation between salinity and DO with prawn abundance and biomass, the abundance and biomass of each sex class of the estuarine prawn *M. equidens* were observed to be greater at the Cua Dai estuary (spatially) and during the dry season (temporally).

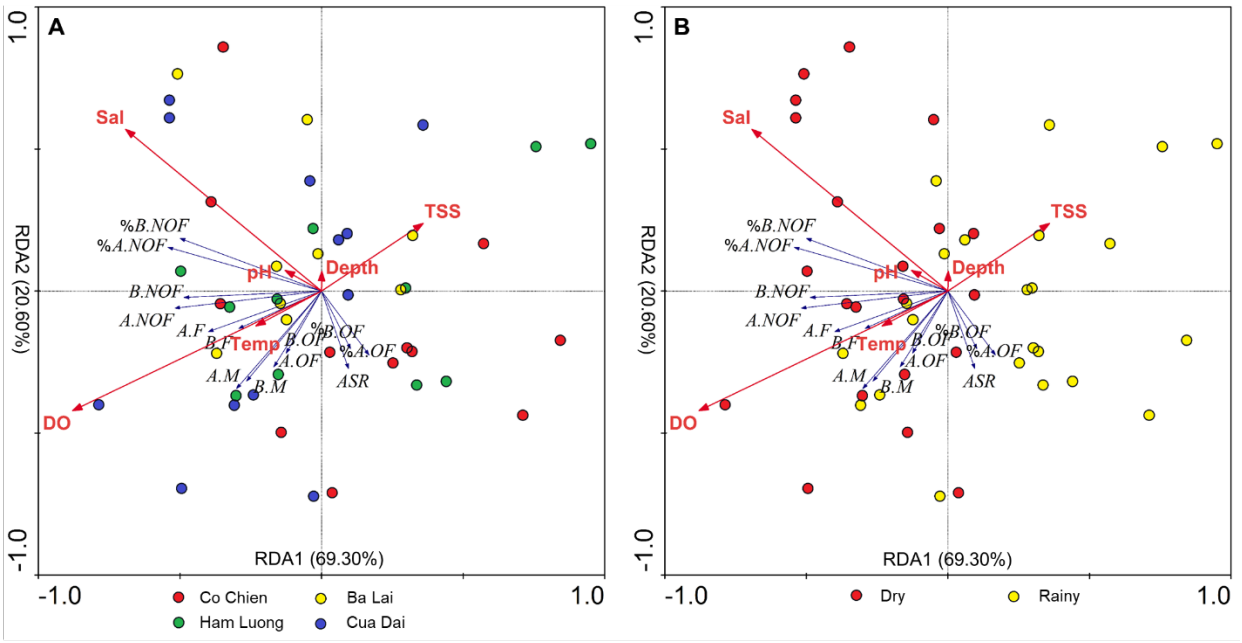

Fig. 9. Triplot of redundancy analysis (RDA) for environmental factors and abundance/biomass of each sex class of the estuary prawn *Macrobrachium equidens* across estuaries (A) and seasons (B). Environmental variables are shown in red and prawn characteristics in blue.

Discussion

Salinity differences between the Ba Lai estuary and other estuaries

The Ba Lai estuary consistently exhibited higher salinity than other estuaries during each survey. A post-hoc Tukey HSD test confirmed that salinity at Ba Lai was significantly different from that of other estuaries, particularly the Co Chien estuary. From the dry to the rainy season, salinity across the Mekong estuaries showed a decreasing trend, attributed to increased rainfall in the upstream Mekong region, which enhanced freshwater discharge, pushed seawater out of the estuary system, and lowered salinity (Le et al., 2006). By the end of the rainy season (in November), while other estuaries maintained low salinity levels, ranging from 0.12 PSU to 1.63 PSU, salinity at Ba Lai began to rise, reaching 7.33 PSU. The elevated salinity levels and distinct pattern of fluctuation at Ba Lai could be explained by the presence of the Ba Lai dam, the only operational irrigation dam in the region, located approximately 12 km from the river mouth.

The Ba Lai dam had been in operation since 2002, with the initial goals of preventing saltwater intrusion, retaining freshwater, and mitigating climate change and sea-level rise. Over more than 20 years of operation, the dam made positive contributions by providing water for domestic use and agricultural production to local residents (Tran et al., 2018). However, several unintended environmental and ecological impacts were observed during its operation. First, the dam caused significant sediment accumulation in the estuary (sediments from other river mouths built up due to the weakened flow at Ba Lai, which was insufficient to transport them away) and within the dam's reservoir due to sediment buildup from upstream sources (Nguyen and Nguyen, 2011; Tran et al., 2021). Second, the accumulation of organic matter and heavy metals in the dam's sediments posed a potential threat to aquatic organisms and humans, as the upstream areas of Ba Lai were used for aquaculture and agriculture (Tran et al., 2021, 2022). These changes affected the community characteristics and distribution patterns of certain aquatic groups, such as free-living nematodes (Nguyen et al., 2020, 2022, 2023; Ngo et al., 2022), benthic macroinvertebrates (Tran et al., 2020), and phytoplankton assemblages (Tran Y et al., 2022).

The salinity fluctuations at the Ba Lai estuary were largely determined by the dam's operation. The dam was completely closed during the dry season and opened twice a month during the rainy season, depending on water management strategies. This distinct salinity pattern, which did not align with the general trend of the Mekong River system, may have stressed estuarine aquatic groups, such as crustaceans, which are naturally adapted to seasonal salinity fluctuations.

Macrobrachium equidens, a typical estuarine prawn in the Mekong estuaries

In this study, despite significant spatial (among estuaries) and temporal (seasonal) fluctuations in salinity that affected the abundance and biomass of female groups (NOF, OF), the estuarine prawn *M. equidens* exhibited a consistent spatial and temporal

pattern in the total abundance of both males and females, suggesting a high degree of adaptability to salinity variation. Seasonal transitions typically lead to changes in biological factors such as predation, competition, and food scarcity (Arimoro and Meye, 2007). As a result, many freshwater prawn species of the genus *Macrobrachium* showed monthly fluctuations in both abundance and biomass. For instance, *M. dux* (Arimoro and Meye, 2007), *M. felicinum* (Inyang, 1981), *M. sirindhorn* (Naiyanetr, 2001), and *M. totonacum* (Mejía et al., 2003). However, in this study, *M. equidens* appeared well-adapted to the constantly changing conditions of the estuarine environment, resulting in minimal seasonal fluctuations in the biomass and abundance of both male and female prawns.

A similar high adaptability has been observed in *M. amazonicum*, a species known for thriving as an exotic species in the Amazon estuary (Lutz et al., 2022). Both *M. equidens* and *M. amazonicum* displayed a higher dominance than other species of the same genus, which may be attributed to their ecological flexibility (Bentes et al., 2014). Their high densities reflect their tolerance to environmental variations, a characteristic common among tropical and subtropical freshwater and brackish water species, which inhabit diverse ecosystems ranging from inland to coastal environments with varying salinity gradients (Pileggi and Mantelatto, 2010).

The mechanisms through which estuarine prawn species, such as *M. equidens*, adapt to salinity fluctuations remain under-researched. However, crustaceans are well known for their ability to cope with salinity changes (Vogt, 2013). Their adaptive mechanisms include: (i) physiological changes, such as adjustments in osmoregulatory function, shifts in ionic content, hemolymph osmolality, gill structural changes, and cell volume regulation (Moshtaghi et al., 2016; Rahi et al., 2018); (ii) biochemical responses, including changes in free fatty acids, amino acids, hemocyte counts, serotonin, and glucose levels (Tantulo et al., 2016); and (iii) genetic responses, involving altered gene expression to regulate protein synthesis (Rahi et al., 2019).

Salinity fluctuations affected sex-specific abundance and biomass

Although the total abundance and biomass of males and females showed little variation across seasons and estuaries, the proportion of non-ovigerous females (NOF) and ovigerous females (OF) fluctuated significantly over time and space. Specifically, the lowest OF abundance percentage was recorded at the Ba Lai estuary (39.44 %), which had the highest salinity levels. The abundance of OF increased from the dry season to the rainy season, while NOF decreased (OF: from 45.15% to 75.87 %, NOF: from 54.85 % to 24.13 %). Biomass percentages followed a similar pattern. Spearman analysis also supported a positive correlation between %NOF and salinity, while %OF showed a negative correlation, suggesting that salinity played a key role in regulating the proportions of non-ovigerous and ovigerous females of *M. equidens* in Mekong estuaries.

Changes in the NOF and OF proportions represented a life strategy of *M. equidens* to adapt to fluctuating salinity in estuarine environments. Although the OF group was present throughout the year, the highest proportion occurred during the rainy season, from August to November, which also coincided with the peak breeding season for *M. equidens*. The impact of salinity on the survival of juvenile palaemonids was also highlighted by Choudhury (1971), who found that *Macrobrachium* species had low salinity tolerance during the larval stage. The high ASR values during the rainy season indicated that males also concentrated in the Mekong estuaries during this time, further reinforcing the idea that these periods marked the peak breeding season for *M. equidens*.

The year-round presence of OF suggested that *M. equidens* was capable of reproducing continuously, indicating that its larvae could tolerate a wide salinity range, from freshwater (0.12 PSU) to polyhaline conditions (22.27 PSU) as found in the Mekong estuaries. However, further laboratory studies were needed to confirm this hypothesis. Another factor supporting the species' ability to reproduce year-round was the stable water temperature. The temperature in the Mekong estuaries remained relatively stable, ranging from 28 °C to 29 °C (Tran et al., 2024), a characteristic feature of tropical coastal estuaries (Carvalho and Couto, 2011) that reflected the thermal consistency of equatorial coastal areas. In contrast to temperate regions, where seasonal temperature changes limited decapod growth and distribution, the steady conditions in tropical zones supported year-round mating and larval development (Costa and Soares-Gomes, 2009).

Management implications

The temporary closure of certain areas within the Mekong estuaries was proposed as a strategy to mitigate the impact of trawling and safeguard endangered species. In this context, understanding the reproductive season is crucial for designing and implementing effective monitoring and conservation strategies (Pacheco et al., 2021). For *M. equidens*, the period of highest production in the Mekong estuaries appears to coincide with the peak of the rainy season, from August to November, as observed in this study. Circular No. 19/2018/TT-BNNPTNT (dated November 15, 2018, issued by the Ministry of Agriculture and Rural Development of Vietnam) provides guidelines for the protection and development of fisheries resources. However, the Mekong estuaries were not included among the areas designated for temporary fishing bans aimed at resource conservation. Given their ecological significance, it is recommended that the Mekong estuaries and their associated mangrove

ecosystems be incorporated into this list. Furthermore, a seasonal closure of the prawn fishery from August to November is suggested to protect not only freshwater and brackish species such as *M. equidens*, but also marine prawn juveniles that rely on estuarine habitats as nurseries.

Annual fisheries resource assessments based on abundances alone may be insufficient for evaluating the population dynamics of specific aquatic species. For instance, this study revealed that the total abundance and biomass of male and female *M. equidens* varied minimally across time and space, indicating that the species is well adapted to estuarine environments. Size distribution, size at sexual maturity, and morphological relationships are potentially useful parameters that could be strengthened in future research to better inform management and conservation efforts for *M. equidens* and other commercially important prawn species, such as the giant freshwater prawn *M. rosenbergii*. Before initiating new fisheries, further studies are needed to clarify the life cycle parameters of these species, encompassing growth, reproduction, recruitment, mortality, spawning locations and timings, nursery habitats, and related biodiversity.

This study also documented several impacts of the Ba Lai Dam on *M. equidens* communities, including a decrease in the proportion of OF and a reduction in the abundance and biomass of OF group. In addition to altering the estuarine salinity regime, the Ba Lai Dam may have induced other ecological changes. For example, the dam likely reduced the flushing rate and restricted water circulation (Chan and Wong, 1993), which may have decreased dissolved oxygen levels and limited larval transport in the area (Wildsmith et al., 2005), leading to a localized reduction in prawn species abundance, biomass, and diversity (Lui et al., 2007). Furthermore, significant accumulation of organic matter in sediment has been reported as a result of flow obstruction by the Ba Lai Dam (Nguyen T and Nguyen M, 2011; Tran et al., 2021), leading to organic enrichment and oxygen depletion from eutrophication (Lee and Arega, 1999), which in turn caused a dramatic decline in species diversity (Lui et al., 2007). Hence, the ecological effects of dams on aquatic ecosystems in the Mekong Delta warrant further investigation.

Conclusion

The species *Macrobrachium equidens* is a typical brackish water prawn found in the Mekong estuaries of Southern Vietnam, known for its high adaptability to fluctuations in salinity within these environments. It can maintain stable population abundance and biomass across different spatial and temporal scales. However, changes in the proportions of non-ovigerous females (NOF) and ovigerous females (OF) reflect a life strategy that allows *M. equidens* to adapt to fluctuating salinity levels in estuarine habitats. *M. equidens* is capable of reproducing year-round, but the peak breeding season occurs during the rainy season, from August to November, which is critical for developing conservation strategies for this species. This emphasizes that the Mekong estuaries possess favourable conditions for the development of young brackish water prawns, serving as key areas for post-larval migration and, consequently, playing a vital role in sustaining freshwater prawn stocks along the Vietnam's southern coastline. Additionally, as Ba Lai is the only estuary with a dam, the ecological effects of dams on aquatic ecosystems require further investigation.

Acknowledgements

This study was funded by the Ben Tre Department of Science and Technology under grant number 1646/HĐ-SKHCN. Thai Thanh Tran was funded by the Master, PhD Scholarship Programme of Vingroup Innovation Foundation (VINIF), code VINIF.2024.TS.050. The authors express gratitude to Mr. Hai Ni for his significant assistance during the river sampling. We also appreciate the insightful feedback from anonymous reviewers that helped enhance the manuscript.

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

Author contributions: Thai Thanh Tran: Conceived and designed the study, conducted fieldwork, collected data, statistical analyses, writing and review of manuscript. Quang Xuan Ngo: Performed statistical analyses, writing and review of manuscript. Phuong Thao Thi Nguyen: Performed statistical analyses, writing and review of manuscript. Luu Thanh Pham: Performed statistical analyses, writing and review of manuscript.

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