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BIODIVERSITY AND GENETIC STRUCTURE OF SHRIMP COMMUNITIES IN THE MEKONG ESTUARINE SYSTEM, VINH LONG PROVINCE

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LIST OF THE PUBLICATIONS RELATED TO THE DISSERTATION

1. **Tran T.T.**, Nguyen T.P.T., Pham T.L., Ngo X.Q., 2025, Spatio-temporal variations in abundance and biomass of three commercial shrimp species in the Mekong estuaries, Southern Vietnam, *Biology Bulletin*, 52(2), 74. https://doi.org/10.1134/S106235902461228X.
2. **Tran T.T.**, Ngo X.Q., Nguyen T.P.T., Pham T.L., 2025, Diversity and distribution of Decapoda and Stomatopoda from the Mekong estuaries in relation to environmental parameters, *Aquatic Sciences,* 87(4), 79. https://doi.org/10.1007/s00027-025-01206-x.
3. **Tran T.T.**, Ngo X.Q., Nguyen T.P.T., Pham T.L., 2025, 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, *Asian Fisheries Science*, 38(3), 143-156. https://doi.org/10.33997/j.afs.2025.38.3.002.
4. **Tran T.T.**, Nguyen T.P.T., Pham T.L., Huynh V.B., Nguyen X.D., Nguyen T.T., Le P.M.C., Ngo X.Q., 2025, The first mitochondrial genome of giant freshwater prawn *Macrobrachium rosenbergii* (Crustacea: Decapoda) from Mekong Delta: Gene characterization and phylogenetic considerations, *Biology Bulletin*, 52(10), 290. https://doi.org/10.1134/S1062359025609334.

INTRODUCTION

1. The urgency

The Mekong River system is one of the world’s largest and most important river basins, playing a critical role in regional ecology, economic development, and the livelihoods of tens of millions of people. In Viet Nam, the Mekong estuarine region includes eight major river mouths, forming a distinctive transitional zone between freshwater and marine environments that supports highly productive estuarine-coastal ecosystems of substantial biological and economic value.

Despite their ecological and socio-economic importance, estuarine ecosystems in the Mekong Delta have received comparatively limited scientific attention. Biological and ecological data remain scarce, particularly regarding the mechanisms regulating ecosystem structure and function under the combined impacts of climate change, pollution, and other anthropogenic pressures, underscoring the urgent need for strengthened baseline research to support integrated management and biodiversity conservation.

Crustaceans, especially shrimp, represent a key ecological and economic component of estuarine ecosystems but remain insufficiently studied. They play essential roles in benthic food webs and nutrient cycling, while several species of high commercial value are facing declines in abundance, population structure, and genetic diversity due to overexploitation, environmental degradation, and climate change, posing significant risks to resource sustainability and local livelihoods.

In this context, the implementation of the dissertation entitled “*Biodiversity and genetic diversity of shrimp assemblages in the Mekong estuarine region, Vinh Long Province*” is both scientifically and practically significant. It aims to clarify genetic characteristics, species diversity, and distribution patterns of shrimp in estuarine ecosystems, providing a scientific basis for conservation and sustainable exploitation, while contributing to crustacean ecology and genetics and supporting adaptive resource management and sustainable livelihoods under climate change.

2. Research objectives

- To preliminarily assess the genetic diversity of several commercially valuable shrimp species in the Mekong estuarine region.
- To evaluate species composition diversity and spatial distribution patterns of shrimp assemblages.
- To investigate the influence of selected surface water environmental factors on the biodiversity of shrimp assemblages.
- To propose solutions for the sustainable exploitation of shrimp resources in the Mekong estuarine region.

3. Research contents

- To establish a genetic diversity database for selected shrimp species using the *COI* gene and the complete mitochondrial genome of giant freshwater prawn (GFP, *Macrobrachium rosenbergii*) in the Mekong estuarine region.
- To analyze species composition structure, density, biomass, biodiversity, and distribution characteristics of shrimp assemblages in the Mekong estuarine region.
- To analyze the effects of selected surface water environmental factors on the biodiversity of shrimp assemblages in the Mekong estuarine region.
- To evaluate spatiotemporal variations in density, biomass, and selected morphological characteristics of GFP, analyze population dynamics, and propose sustainable exploitation strategies for this resource.

4. Scientific and practical significance

4.1. Scientific significance

The dissertation advances knowledge of estuarine aquatic ecology through integrated analyses of shrimp community structure, biodiversity, and spatiotemporal dynamics, improving theoretical understanding of benthic organism responses to environmental gradients in freshwater-marine transition zones.

By linking shrimp assemblage characteristics with environmental parameters, the study elucidates mechanisms governing distribution and adaptation under highly variable estuarine conditions, contributing to ecological theory and supporting ecosystem management and forecasting in the lower Mekong River.

In addition, the dissertation provides scientific evidence on the structure, diversity, and genetic relationships of commercially important shrimp species, strengthening the theoretical basis for aquatic genetic resource conservation and demonstrating the effectiveness of an interdisciplinary approach combining ecology, morphology, and genetics.

4.2. Practical significance

The research provides essential baseline environmental and ecological data to support integrated management, ecological planning, and responses to salinity intrusion, pollution, and climate change in the Mekong estuarine region.

Genetic analyses using molecular markers supply key scientific evidence for the conservation, selective breeding, and restoration of well-adapted indigenous shrimp strains, contributing to the sustainability of estuarine aquaculture.

Baseline information on species diversity, distribution, and genetic structure underpins fisheries monitoring and management, while population dynamic analyses of GFP support the identification of sustainable harvesting thresholds and the maintenance of stable livelihoods for local fishing communities.

Chapter 1. LITERATURE REVIEW

1.1. Overview of estuarine ecosystems

1.1.1. Definition

An estuary is a transitional zone where seawater intrudes into a river up to the maximum limit of tidal influence. This system is commonly divided into three zones: the lower estuary (strongly influenced by marine conditions), the middle estuary (characterized by intensive mixing of freshwater and saline water), and the upper estuary (predominantly freshwater but still subject to tidal effects). The boundaries between these zones vary depending on river discharge and tidal regimes.

1.1.2. Basic characteristics of estuarine ecosystems

1.1.2.1. Diversity of integrated sub-ecosystems

Estuarine ecosystems exhibit high biodiversity due to the integration of multiple habitats, including tidal flats, tidal channels, shallow waters, and wetlands. Organisms not only adapt to these habitats but also actively modify them, thereby enhancing overall ecosystem diversity.

Estuarine trophic systems are highly complex, with detrital food webs playing a dominant role. Biomass derived from mangroves, seagrasses, and benthic algae is largely not consumed directly but is decomposed into detritus, which serves as a primary energy source for benthic fauna and higher trophic levels. Concurrently, phytoplankton- and microbe-based food webs contribute to a multi-source trophic system that is tightly interconnected.

1.1.2.3. Adaptation of organisms to estuarine environmental conditions

Estuarine environments are characterized by strong fluctuations in salinity, temperature, oxygen concentration, and nutrient availability, among which salinity is the most influential controlling factor. Estuarine organisms adapt through physiological regulation or tolerance of internal state changes, often employing a flexible combination of both strategies. Although environmental variability tends to reduce species richness, estuarine ecosystems maintain high organismal density and biomass due to high primary productivity and relatively low predation pressure.

1.1.3. The Mekong estuarine ecosystem

1.1.3.1. Environmental and hydrological conditions

The Mekong River is characterized by high discharge and a stable seasonal flood regime, forming the ecological foundation of the downstream region. Natural drivers such as floods, tides, and monsoons regulate salinity, facilitate nutrient transport, and sustain biological processes within the estuarine system.

This system is strongly influenced by substantial sediment and organic matter loads from upstream, which provide the primary energy source for detritus-based food webs. Annual floods not only transport sediments but also sustain delta accretion and maintain the ecological functions of coastal zones.

The Mekong Delta is a multi-branch estuarine system simultaneously influenced by tides from both the East Sea and the West Sea, resulting in complex hydrodynamic conditions. Salinity exhibits pronounced seasonal variability, with deep inland saltwater intrusion during the dry season and freshwater-driven salinity displacement toward the sea during the rainy season.

1.1.3.2. Aquatic organisms in the mekong estuary

The Mekong estuary harbors the highest biodiversity within the river basin due to the mixing of marine, brackish, and freshwater organisms. Mangrove forests play a crucial role as spawning and nursery grounds for numerous fish and invertebrate species.

While estuarine fish communities have been relatively well studied, invertebrate groups, particularly crustaceans and benthic fauna, remain poorly documented. Recent studies indicate that decapod crustaceans dominate the assemblage but occur at relatively low densities, reflecting pressures from exploitation and habitat degradation. Overall, research on estuarine crustacean assemblages in the Mekong remains limited and requires further investigation.

1.2. Biodiversity of estuarine shrimp assemblages

1.2.1. Genetic diversity

1.2.1.1. General overview

Assessment of genetic diversity provides a critical basis for the conservation and sustainable management of shrimp resources. Traditional morphological taxonomy faces limitations due to morphological similarity among species and ontogenetic variation across developmental stages. The integration of morphological approaches with molecular markers, particularly mitochondrial genes, has proven effective in species identification, phylogenetic analysis, and population structure assessment, thereby improving the accuracy of biodiversity evaluation.

1.2.1.2. Viet Nam

In Viet Nam, studies on shrimp genetic diversity remain limited and have primarily focused on the GFP. Existing results indicate clear genetic differentiation among populations; however, most studies are single-species oriented. Genetic relationships among shrimp species within assemblages, particularly in the Mekong Delta, have yet to be clarified, highlighting the need for more systematic and comprehensive research.

1.2.2. Species composition diversity

1.2.2.1. General overview

Shrimps are widely distributed across aquatic environments, with approximately 4,000 species recorded worldwide. The suborder Penaeoidea, particularly the family Penaeidae, dominates in terms of economic value, whereas the suborder Caridea contains a greater number of species, including many freshwater taxa within the families Atyidae and Palaemonidae. Numerous species are believed to remain undescribed, especially in tropical regions.

1.2.2.2. Viet Nam

Research on shrimp assemblages in Viet Nam began in the late nineteenth century but has been spatially uneven. Approximately 24 species of freshwater prawns have been recorded, primarily belonging to the genus

Macrobrachium. For brackish and marine shrimps, surveys have documented over 230 species; however, most studies have focused on northern and central regions. The Mekong Delta remains deficient in systematic studies on shrimp assemblages and their ecology in natural environments.

1.2.2.3. The Mekong estuary

Shrimp assemblages in the Mekong estuary exhibit relatively high diversity, including marine, brackish, and salinity-tolerant freshwater species. Many species of high economic value play a vital role in coastal livelihoods. However, most existing studies remain limited to species composition descriptions, lacking in-depth analyses of genetic diversity, ecological characteristics, and adaptive mechanisms in response to environmental variability.

1.3. Interactions between shrimp assemblages and environmental conditions

1.3.1. Flow regime and sediments

Hydrodynamic conditions strongly influence sediment structure and shrimp habitats. Fine sandy substrates rich in mud and organic matter generally support higher shrimp densities, particularly during juvenile stages.

1.3.2. Water depth

Juvenile shrimps are typically distributed in shallow waters, whereas adults inhabit deeper zones, reflecting ontogenetic niche differentiation.

1.3.3. Temperature and salinity

Temperature and salinity exert strong influences on shrimp activity, distribution, and growth. Juvenile shrimps generally exhibit greater tolerance to low and fluctuating salinity compared to adults.

1.3.4. Dissolved oxygen

Hypoxic conditions cause shrimps to avoid affected areas or emerge from sediments. Overall, hydrological factors and water quality parameters strongly regulate the structure and dynamics of shrimp assemblages. However, studies in the Mekong Delta still lack quantitative analyses of these relationships.

1.4. Threats to shrimp assemblages

1.4.1. Upstream hydropower development

Hydropower dams fragment habitats and alter flow and flood regimes, adversely affecting shrimp migration, reproduction, and natural nursery grounds.

1.4.2. Land-use change and deforestation

The decline of mangrove forests results in the loss of critical habitats and increased erosion, disrupting aquatic food webs.

1.4.3. Industrial, agricultural, and aquaculture development

Pollution and the reduction of seasonally flooded areas strongly impact sensitive life stages of shrimps, while invasive species pose risks of altering community structure.

1.4.4. Overexploitation

Destructive fishing practices and high exploitation intensity rapidly deplete populations, destroy spawning grounds, and reduce genetic diversity.

1.4.5. Climate change

Climate change disrupts rainfall-flood regimes and the biological rhythms of shrimps, particularly in estuarine regions.

Shrimp assemblages in the Mekong Delta are currently subject to multiple cumulative pressures, among which overexploitation is the most urgent. The lack of information on population structure and recovery potential increases the risk of resource depletion. Therefore, comprehensive studies, particularly on high-value species such as GFP, are essential to support sustainable management and conservation under ongoing environmental and climatic changes.

Chapter 2. MATERIALS AND METHODS

2.1. Research objects

This study focuses on evaluating the relationships between selected surface water environmental parameters and the growth, structure, and dynamics of shrimp assemblages at four Mekong River estuaries in Vinh Long Province, including Dai, Ba Lai, Ham Luong, and Co Chien estuaries. In addition, community characteristics, genetic diversity, and shrimp resources were analyzed, with the GFP, serving as the focal species.

2.2. Research methods

2.2.1. Study area and sampling period

The study area was located in the estuarine zones of the Tien River, encompassing the Dai, Ba Lai, Ham Luong, and Co Chien estuaries. At each estuary, two sampling sites were established: CD1 and CD2 at Dai estuary; BL1 and BL2 at Ba Lai estuary; HL1 and HL2 at Ham Luong estuary; and CC1 and CC2 at Co Chien estuary (Fig 2.1). Shrimp assemblages and environmental parameters were sampled and measured in 2022 during March (dry season), June (dry-rainy season), August (rainy season), and November (rainy- dry season). For analytical and interpretative purposes, the data were subsequently grouped into two seasons: the dry season (March and June) and the rainy season (August and November).

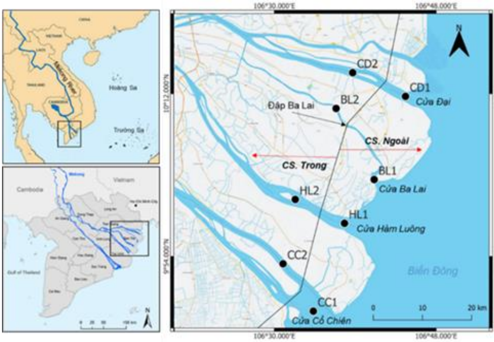

Figure 2.1. Map of the study area and shrimp assemblage sampling sites in the Mekong estuarine region

2.2.2. Data collection

2.2.2.1. Shrimp sampling, biomass measurement, and species identification

At each sampling site, four replicate bottom trawl hauls were conducted using a shrimp trawl net with a mouth width of 4 m, a length of 6 m, and a mesh size of 20 mm. After collection, specimens were preserved in 96% ethanol and transported to the laboratory of the Institute of Life Sciences for further analysis.

Individual shrimp body weight was measured using an electronic balance with a precision of ±0.01 g and corrected by a coefficient of 1.2 to compensate for weight changes due to ethanol preservation. Shrimp specimens were identified based on morphological characteristics through comparison with standard taxonomic references, including Holthuis (1980), Chaitiamvong and Supongpan (1992), Nguyen Van Thuong and Truong Quoc Phu (2004), and Dang Ngoc Thanh and Ho Thanh Hai (2012).

2.2.2.2. Measurement of environmental parameters

Surface water environmental parameters were measured concurrently with shrimp sampling, including temperature, salinity, pH, dissolved oxygen (DO), total suspended solids (TSS), and water depth.

2.2.3. Data processing and analysis

2.2.3.1. Genetic diversity of shrimp assemblages and the mitochondrial genome of GFP

Pleopod tissue samples from selected shrimp species were collected and preserved for DNA extraction using a commercial extraction kit. A fragment of the mitochondrial cytochrome c oxidase subunit I (*COI*) gene (~720 bp) was amplified by PCR using the universal primers described by Folmer et al. (1994). PCR products were verified by electrophoresis on 1% agarose gels and subsequently sequenced.

COI sequences were compared against the GenBank database using BLAST to assess sequence similarity, and phylogenetic trees were constructed using the Maximum Likelihood method with bootstrap support

(1,000 replicates). Genetic diversity of six commercially important shrimp species was assessed using haplotype diversity (H_d) and nucleotide diversity (π) indices calculated in DnaSP software.

For GFP, the complete mitochondrial genome was sequenced using next-generation sequencing (NGS) technology (Illumina MiSeq). The mitochondrial genome was assembled de novo using GetOrganelle, annotated with MITOS, and manually curated using MEGA X. Nucleotide composition, skewness, codon usage, tRNA secondary structure, and mitochondrial genome maps were comprehensively analyzed using specialized bioinformatics tools. A phylogenetic tree based on 13 protein-coding genes (PCGs) from 12 species of the family Palaemonidae (with two outgroup species) was constructed using the Maximum Likelihood method, revealing clear evolutionary relationships among the shrimp species examined.

2.2.3.2. Characteristics of shrimp assemblages

For shrimp assemblages, density and biodiversity indices (species richness S, Margalef's index d, Shannon-Wiener index H', and Pielou's evenness J') were calculated using PRIMER v6.1. A three-factor PERMANOVA (season, estuary, and sampling site) was applied to assess differences in shrimp community structure, with homogeneity of multivariate dispersion tested using PERMDISP.

Spatial and temporal distribution patterns of shrimp assemblages were visualized using nmMDS plots. SIMPER analysis was employed to identify species contributing most to differences among groups. Relationships between environmental variables and shrimp assemblages were evaluated using DistLM, BIOENV, RDA, and Spearman rank correlation to identify key environmental drivers influencing community structure. These analyses were conducted using PRIMER v6 with PERMANOVA add-on, CANOCO 4.5, and Stat 18 software.

2.2.3.3. Relationships between environmental factors and shrimp assemblages

Environmental variables were initially screened using Draftsman plots to assess data distribution and collinearity, followed by PCA to identify major environmental gradients. A three-factor PERMANOVA (season, estuary, and sampling site) was then applied to test differences among groups using standardized data and Euclidean distance matrices.

DistLM and BIOENV analyses were employed to assess the effects of individual environmental variables and combinations of variables on shrimp assemblage structure. DistLM results were visualized using dbRDA plots. In addition, RDA and Spearman rank correlation were applied to evaluate relationships between species density, assemblage characteristics, and environmental factors.

2.2.3.4. Morphological characteristics and population dynamics of GFP

A total of 187 female GFP individuals were measured for 20 morphological traits and body weight, with carapace length (CL) used as the standard reference variable. PCA was applied to identify key morphological traits and to evaluate spatial and temporal patterns of morphological variation. Overall morphological differences were tested using a two-factor PERMANOVA with season and estuary as fixed factors.

Univariate analyses (ANOVA or Kruskal-Wallis tests) were conducted to examine differences in individual morphological traits, followed by appropriate post hoc comparisons. Relationships between morphological traits and environmental variables were assessed using Spearman rank correlation analysis.

Length-length and length-weight relationships were established to determine growth patterns (isometric or allometric). Population growth parameters were estimated using the von Bertalanffy growth model implemented in FiSAT II software. Mortality parameters, including total mortality (Z), natural mortality (M), and fishing mortality (F), as well as recruitment patterns, relative yield per recruit (Y’/R), and relative biomass per recruit (B’/R), were calculated to evaluate exploitation status and the sustainability of GFP populations.

Chapter 3. RESULTS AND DISCUSSION

3.1. Initial development of a genetic diversity database for selected shrimp species using the *COI* gene and the mitochondrial genome of GFP in the Mekong estuary

3.1.1. Genetic diversity and relationships of economically important shrimp species

Analysis of genetic relationships based on the *COI* gene revealed clear genetic differentiation between species belonging to the family Penaeidae and Palaemonidae. Clear genetic separation was also observed among genera within the same family, as demonstrated by the genera *Metapenaeus* and *Parapenaeopsis* within the family Penaeidae. Furthermore, substantial differences in *COI* gene structure were detected among species within the same genus, such as between *M. rosenbergii* and *M. equidens* (genus *Macrobrachium*), between *M. ensis* and *M. brevicornis* (genus *Metapenaeus*), and between *P. hardwickii* and *P. sculptilis* (genus *Parapenaeopsis*). The haplotype diversity index (H_d) reflects haplotype richness, whereas nucleotide diversity (π) represents the degree of genetic divergence at the nucleotide level. However, when sample size is limited, estimates of genetic diversity based on H_d may be less reliable.

3.1.2. Characteristics of the mitochondrial genome of GFP from the Mekong estuary

3.1.2.1. Sample quality assessment and WGS library preparation

The results of DNA quality assessment were as follows: DNA concentration (ng/µL): 30.20; OD260/OD280: 1.65; total DNA amount (ng): 1510. Library quality parameters included a library concentration of 41.70 ng/µL and an average fragment size of 470 bp. These results satisfied the requirements for sequencing in terms of both concentration and fragment length.

3.1.2.2. Structure of the mitochondrial genome of GFP from the Mekong estuary

The mitochondrial genome of the Mekong GFP is circular and 15,766 bp in length, comprising 37 genes, including 13 protein-coding genes (PCGs), 22 transfer RNA genes, and two ribosomal RNA genes, as well as one control region. The total length of the PCGs is 11,057 bp, accounting for 70.13% of the entire mitochondrial genome. Among the 13 PCGs, gene length ranges from 159 bp (*ATP8*) to 1,677 bp (*NAD5*). Nine genes (*COX1*, *COX2*, *ATP8*, *ATP6*, *COX3*, *NAD3*, *NAD6*, *CYTB*, and *NAD2*) are encoded on the heavy (H) strand, whereas the remaining four genes (*NAD5*, *NAD4*, *NAD4L*, and *NAD1*) are located on the light (L) strand. The PCGs encode a total of 5,255 amino acids, of which leucine (Leu) is the most abundant (11.30%), followed by serine (Ser, 10.66%), threonine (Thr, 7.75%), and lysine (Lys, 7.06%).

The mitochondrial genome contains 22 tRNA genes with lengths ranging from 62 bp ($tRNA^{Arg}$) to 69 bp ($tRNA^{Glu}$, $tRNA^{Ser2}$, and $tRNA^{Trp}$), with a total length of 1,450 bp. All tRNAs exhibit the typical cloverleaf secondary structure, except for $tRNA^{Ser1}$, in which the DHU arm is replaced by a simple loop, a feature commonly observed in many crustacean species.

Previously reported mitochondrial genomes of the family Palaemonidae exhibit two distinct gene arrangement patterns. The first group, comprising species of the genus *Macrobrachium*, displays a gene order consistent with the ancestral Pancrustacea pattern: 5'-$NAD4L$-$tRNA^{Thr}$-$tRNA^{Pro}$-$NAD6$-3'. The second group, including species of the genera *Palaemon* and *Exopalaemon*, shows a gene rearrangement involving a transposition between $tRNA^{Pro}$ and $tRNA^{Thr}$, resulting in the gene order: 5'-$NAD4L$-$tRNA^{Pro}$-$tRNA^{Thr}$-$NAD6$-3'.

3.1.2.3. Phylogenetic relationships within the family palaemonidae based on mitochondrial genomes

Phylogenetic analysis based solely on protein-coding genes from 16 mitochondrial genomes representing three genera (*Palaemon*, *Exopalaemon*, and *Macrobrachium*) indicated that *Exopalaemon* and *Palaemon* are closely related evolutionarily. In contrast, the genus *Macrobrachium* forms a distinct monophyletic clade.

3.2. Diversity of shrimp communities in the Mekong estuary

3.2.1. Species composition diversity

3.2.1.1. Structure of species composition

The shrimp community comprised 62 species belonging to 18 genera and seven families (Alpheidae, Atyidae, Palaemonidae, Palinuridae, Penaeidae, Sergestidae, and Squillidae), distributed across two orders: Decapoda and Stomatopoda. The order Decapoda overwhelmingly dominated the community, with 12,846 individuals, accounting for 97.75% of the total abundance, whereas Stomatopoda was represented by only 296 individuals (2.25%), all belonging to the family Squillidae. The family Palaemonidae was the most dominant, with 7,100 individuals (54.03%), followed by Penaeidae with 5,252 individuals (39.96%). Together, these two families accounted for 93.99% of the total abundance. The remaining families, Sergestidae, Alpheidae, Atyidae, and Palinuridae, contributed relatively small proportions to the community.

3.2.1.2. Density and biomass

Mean total density ranged from 38.62±34.44 ind/1,000 m^2 (CC2) to 194.86±271.85 ind/1,000 m^2 (CD1). Mean total biomass varied from 211.30±247.48 g/1,000 m^2 (CC2) to 625.34±660.04 g/1,000 m^2 (CD2). Mean individual biomass ranged from 2.86±1.72 g/1,000 m^2 (BL1) to 5.30±3.50 g/1,000 m^2 (CC2), while the mean W index ranged from -0.05±0.16 (BL2) to 0.20±0.23 (CC2). Despite differences in sampling methods, overall density and biomass in the Mekong Estuary were higher than those reported for several other regions worldwide.

3.2.1.3. Biodiversity indices

Mean values of species richness (S) ranged from 4.75±1.61 to 8.50±2.59, Margalef's index (d) from 0.87±0.37 to 1.59±0.45, Shannon-Wiener index (H') from 0.85±0.39 to 1.54±0.30, and Pielou's evenness index (J') from 0.50±0.22 to 0.81±0.12. Sites HL2 and BL2 exhibited relatively low biodiversity, whereas CC1 and CD1 showed higher diversity. According to S and d indices, HL2 had the lowest diversity; however, when evenness (H′ and J') was considered, BL2 (within Ba Lai Dam) exhibited the lowest biodiversity. Overall, biodiversity in the Mekong Estuary shrimp community was higher than that reported in several other regions.

3.2.1.4. Representative species

SIMPER analysis identified 13 shrimp species with the highest contributions to community similarity across spatial (estuary, sampling area) and temporal (season) scales. These species belonged to four families, Palaemonidae, Alpheidae, Penaeidae, and Squillidae, with Palaemonidae and Penaeidae playing dominant roles. Species of the genera *Macrobrachium* (Palaemonidae) and *Parapenaeopsis* and *Metapenaeus* (Penaeidae) contributed most substantially to community similarity across spatiotemporal gradients.

3.2.2. Spatial and temporal distribution diversity

3.2.2.1. Spatial distribution (among estuaries)

Mean shrimp density at the Co Chien estuary (79.31±81.45 ind/1,000 m^2) was lower than at the other estuaries, ranging from 124.63±89.94 ind/1,000 m^2 at Ba Lai to 163.50±211.15 ind/1,000 m^2 at Cua Dai. Similarly, mean total biomass was lowest at Co Chien (290.20±237.16 g/1,000 m^2) and relatively low at Ba Lai (346.36±395.36 g/1,000 m^2), whereas Ham Luong and Cua Dai exhibited higher mean total biomass, at 424.22±322.70 g/1,000 m^2 and 516.11±533.59 g/1,000 m^2, respectively. Mean individual biomass, mean W index, and biodiversity indices were lowest at Ba Lai and highest at Co Chien and Cua Dai. For example, mean W at Ba Lai was 0.0014±0.16, compared with 0.15±0.21 at Co Chien. Likewise, mean H' and J' at Ba Lai were the lowest (1.06±0.46 and 0.57±0.22), whereas at Co Chien they reached 1.38±0.44 and 0.80±0.10, respectively.

3.2.2.2. Spatial distribution (sampling zones)

Mean individual biomass within estuaries was higher than that outside estuaries (4.77±3.42 g/1,000 m^2 vs. 3.69±2.57 g/1,000 m^2). Mean W index values were positive both inside and outside estuaries (0.08±0.21 and 0.06±0.17, respectively). However, statistical analyses indicated no significant differences between sampling zones in mean individual biomass or mean W index. In contrast, mean total density, mean total biomass, and biodiversity indices (S, d, H’, and J’) differed significantly between zones. Specifically, mean total density and biomass outside estuaries were higher than those inside estuaries, with values of 155.95±166.74 ind/1,000 m^2 and 441.17±364.22 g/1,000 m^2 outside, compared with 87.41±84.23 ind/1,000 m^2 and 352.43±402.52 g/1,000 m^2 inside estuaries. Similarly, biodiversity indices were consistently higher outside estuaries (S = 8.07±2.79; d = 1.51±0.49; H’ = 1.45±0.39; J’ = 0.72±0.15) than inside estuaries (S = 5.48±2.13; d = 1.10±0.46; H’ = 1.09±0.39; J’ = 0.67±0.19). Overall, shrimp assemblages outside estuaries exhibited significantly higher density, biomass, and biodiversity than those inside estuaries.

3.2.2.3. Temporal distribution (seasonal variation)

Mean total shrimp density during the dry season (140.19±165.81 ind/1,000 m^2) was higher than during the rainy season (103.19±95.39 ind/1,000 m^2). Pielou’s evenness index (J’) was also slightly higher in the dry season (0.71±0.14) than in the rainy season (0.68±0.20). PERMANOVA results indicated no statistically significant seasonal differences in mean total density or J’. Mean individual biomass in the dry and rainy seasons was 4.49±2.98 and 3.97±3.15 g/1,000 m^2, respectively; however, the evidence was insufficient to conclude a significant seasonal difference in individual biomass.

3.3. Effects of surface water environmental factors on shrimp assemblage biodiversity in the Mekong estuary

3.3.1. Surface water environmental characteristics of the Mekong estuary

Mean pH values differed significantly among seasons, estuaries, and sampling zones. Mean pH in the dry season (7.49±0.35) was higher than in the rainy season (7.19±0.37).

Mean temperature did not differ significantly between sampling zones but varied significantly among seasons and estuaries. Water temperature in the Mekong estuary was relatively stable, ranging from 29.5°C to 30.5°C.

Mean dissolved oxygen (DO) showed significant differences only between sampling zones, with higher values outside estuaries (6.60±0.38 mg/L) than inside estuaries (6.25±0.38 mg/L).

Salinity showed strong spatial and seasonal variation, ranging from 0.06 PSU in the rainy season to 22.63 PSU in the dry season. Mean salinity was markedly higher in the dry season than in the rainy season, and higher outside estuaries than inside estuaries. Among estuaries, Cua Dai and Ba Lai exhibited higher mean salinity than Ham Luong and Co Chien; however, these differences were not statistically significant.

Mean water depth differed significantly among estuaries, being lowest at Ham Luong (5.03±2.42 m) compared with Ba Lai (8.16±4.17 m) and Cua Dai (7.68±3.31 m). In addition, mean depth outside estuaries (5.70±2.56 m) was lower than inside estuaries (7.50±4.40 m).

Total suspended solids (TSS) were substantially higher in the rainy season (89.26±69.90 mg/L) than in the dry season (61.08±37.81 mg/L).

3.3.2. Effects of environmental factors on the shrimp community structure in the Mekong estuaries

When data from both seasons were considered together, dissolved oxygen (DO) and salinity were identified as the most influential environmental variables governing the characteristics of the shrimp community. Both variables showed positive correlations with shrimp density, biomass, and biodiversity indices, indicating their key role in structuring estuarine shrimp assemblages.

3.3.3. Effects on the spatio-temporal distribution of the shrimp community in the Mekong estuaries

3.3.3.1. Spatio-temporal variability of the shrimp community

Shrimp communities in the Mekong estuarine system showed clear spatio-temporal variation. Ba Lai estuary had lower density, biomass, biodiversity, and a distinct community structure compared with other estuaries, likely due to hydrological changes caused by the Ba Lai dam.

Overall, shrimp density, biomass, and biodiversity were higher in the outer estuary than the inner estuary, and higher in the dry season than the rainy season. Salinity and its seasonal variation were the main drivers of these patterns, with community variation primarily explained by survey zone, followed by season and, to a lesser extent, estuary-level differences.

3.3.3.2. Distribution of ecological groups

Based on multivariate interactions between 13 representative shrimp species and environmental variables, with particular emphasis on salinity, the dominant shrimp species could be classified into four major ecological groups:

- Salinity-oriented estuarine shrimp: species showing a strong and statistically significant positive correlation with salinity;
- Typical estuarine shrimp with salinity preference: species exhibiting a positive and statistically significant correlation with salinity;
- Typical estuarine shrimp: species showing a positive but non-significant correlation with salinity;
- Freshwater-oriented estuarine shrimp: species displaying a strong and statistically significant negative correlation with salinity.

3.4. Variations in density, biomass, morphology, population characteristics, and proposed sustainable exploitation measures for GFP in the Mekong estuaries

3.4.1. Density, biomass, and morphology of GFP in the Mekong estuaries

3.4.1.1. Density and biomass

The Ba Lai and Co Chien estuaries exhibited relatively low mean total densities of GFP, with values of 1.75±2.62 ind/1,000 m^2 and 2.63±4.64 ind/1,000 m^2, respectively. In contrast, the Ham Luong estuary recorded a higher mean total density of 5.19±5.23 ind/1,000 m^2. Mean total density was higher in the inner estuarine zone (4.70±5.84 ind/1,000 m^2) than in the outer estuarine zone (2.00±3.56 ind/1,000 m^2). No statistically significant seasonal difference was detected in mean total density, with values of 3.96±5.89 ind/1,000 m^2 during the dry season and 2.74±3.89 ind/1,000 m^2 during the rainy season.

Mean total biomass and mean individual biomass differed significantly only between survey zones. Specifically, the inner estuarine zone exhibited higher mean total biomass and mean individual biomass (134.62±184.70 g/1,000 m^2 and 21.43±18.54 g/1,000 m^2, respectively) compared to the outer estuarine zone (65.03±117.77 g/1,000 m^2 and 14.85±21.07 g/1,000 m^2, respectively). No significant differences in mean total biomass or mean individual biomass were observed among estuaries or between seasons.

3.4.1.2. Morphology

All morphological traits of GFP were higher during the rainy season than during the dry season, with the exception of CaW, indicating that individuals generally attained larger body size and weight in the rainy season. Although all morphological measurements at the Ba Lai estuary were lower than those recorded at the other estuaries, statistical analyses indicated no significant differences in morphological traits among estuaries.

3.4.2. Effects of selected surface-water environmental factors on density, biomass, and morphology of GFP in the Mekong estuaries

3.4.2.1. Density and biomass

Spearman correlation analysis revealed that none of the examined environmental variables showed significant correlations with the density or biomass of GFP in the Mekong estuaries. These results suggest that the species is highly tolerant and well adapted to estuarine environmental conditions.

3.4.2.2. Morphology

Spearman correlation analysis indicated that temperature and total suspended solids (TSS) exhibited little to no significant correlation with morphological traits of GFP. In contrast, pH, salinity, dissolved oxygen (DO), and water depth showed significant correlations with several morphological traits. Specifically, pH and salinity were negatively correlated with body traits, whereas water depth exhibited positive correlations. However, correlation coefficients for depth were relatively low ($r = 0.14$-0.21), as were those for pH and salinity ($r = 0.15$-0.20), which were significant only for body-related traits.

Among the examined variables, DO exerted the strongest influence on morphology, with correlation coefficients ranging from 0.23 to 0.36, and was the only factor showing significant correlations with all measured morphological traits of GFP.

3.4.3. Population dynamics and proposed sustainable exploitation measures

3.4.3.1. Asymptotic length (L∞) and growth coefficient (K)

The estimated asymptotic length for female individuals was $L_\infty = 253.25$ mm, with a growth coefficient $K = 0.59$ yr^{-1} and $t_0 = -0.051$ (the theoretical age at which length equals zero). The maximum age (t_{max}), estimated from the growth model, was 5.03 years. Accordingly, the von Bertalanffy growth equation describing population growth of GFP in the Mekong estuaries was: $L_t = 253.25 \times (1 - e\hat{}(-0.59(t + 0.051)))$.

3.4.3.2. Recruitment

Recruitment represents the entry of juvenile individuals into the exploitable population once they reach a sufficient size or age. Recruitment of GFP in the Mekong estuaries occurred almost year-round, with a pronounced increase from April to August and peak recruitment in April and May, accounting for 19% and 22% of total recruitment, respectively.

3.4.3.3. Mortality estimates

The estimated total mortality (Z), natural mortality (M), and fishing mortality (F) were $Z = 3.59\ yr^{-1}$ (CI: 2.8-4.38), $M = 0.72\ yr^{-1}$, and $F = 2.87\ yr^{-1}$. These results indicate that natural mortality of GFP in the Mekong estuaries is relatively low, reflecting favorable environmental conditions, whereas fishing mortality is exceptionally high.

3.4.3.4. Proposed sustainable exploitation measures for GFP in the Mekong estuaries

The fishing season for GFP in the Mekong estuaries is recommended to begin in the second half of April and end around July each year. During the fishing season, a sustainable exploitation strategy is proposed that includes increasing the length at first capture to at least 60% of $L\infty$ ($Lc \geq 151.95$ mm) and maintaining exploitation rates not exceeding $E = 0.5$. This approach aims to ensure stable yields while preserving the long-term reproductive capacity of the population. However, in cases where short-term economic considerations for fishers must be prioritized, a threshold of $Lc/L\infty = 0.5$ ($Lc \geq 126.6$ mm) may be considered acceptable.

CONCLUSIONS AND RECOMMENDATIONS

Conclusions

Genetic analyses revealed clear differentiation between penaeid shrimp (Penaeidae) and palaemonid shrimp (Palaemonidae), as well as among genera and species within the same family. Under conditions of limited sample size, nucleotide diversity (π) was found to be a more reliable indicator of genetic diversity than haplotype diversity (H_d).

The shrimp community in the Mekong estuaries is characterized by high abundance and species richness, with pronounced spatio-temporal variability in community structure. The community can be classified into four major ecological groups: salinity-oriented estuarine shrimp, freshwater-oriented estuarine shrimp, typical salinity-preferring estuarine shrimp, and typical estuarine shrimp. Among the environmental factors examined, salinity and dissolved oxygen were identified as the primary drivers governing spatial and temporal variation in shrimp communities.

Morphological variation in GFP occurred mainly on a seasonal basis, with larger body size observed during the rainy season. Among the examined environmental variables, dissolved oxygen was the most influential factor affecting prawn morphology. Recruitment occurred throughout the year, with a pronounced peak from April to August, particularly in April-May. However, the results indicate that the stock is currently subjected to excessive fishing pressure.

Recommendations

Future genetic diversity assessments should increase sample size (10-30 inds) and incorporate samples from a wider range of aquatic habitats. In addition to H_d and π, future studies should assess haplotype number, haplotype networks, and genetic differentiation (FST) among shrimp populations across geographic regions within the Mekong Delta and globally.

Further analyses should examine the effects of additional environmental variables, particularly sediment-related factors such as nutrients (TN, OM, Chl, NH_4^+, NO_3^-, NO_2^-, PO_4^{3-}), sediment composition, and river discharge, on shrimp community characteristics.

Future studies are encouraged to apply geometric morphometric approaches based on landmark analysis, which can detect fine-scale morphological differences at microgeographical scales, such as among Mekong estuaries.

Recommended sustainable exploitation measures for GFP resources in the Mekong estuaries include limiting the fishing season from the second half of April to approximately July each year, increasing the length at first capture to $Lc \geq 151.95$ mm, and maintaining exploitation rates at or below E

= 0.5. In cases where economic priorities for fishers must be considered, a minimum capture length of Lc ≥ 126.6 mm may still be acceptable.

NEW CONTRIBUTIONS OF THE DISSERTATION

The dissertation provides first-time genetic data for several commercially important shrimp species, particularly the complete mitochondrial genome of GFP, clarifying genetic relationships, population differentiation, and evolutionary patterns within Palaemonidae to support conservation and management of native shrimp resources.

It supplies new baseline data on shrimp community structure in the Mekong estuarine region, including species composition, density, biomass, biodiversity, and spatiotemporal distribution, contributing to ecological research and environmental management in freshwater-marine transitional zones.

For the first time, the study analyzes relationships between shrimp community characteristics and environmental factors, elucidating distribution patterns and adaptive responses under highly dynamic estuarine conditions.

The dissertation also presents the first assessment of wild GFP population dynamics in the Mekong estuaries, estimating growth parameters and sustainable exploitation levels to inform resource management and sustainable harvesting strategies.