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A Multi-Scale Assessment of Estuarine Fish Communities in Irrawaddy Delta

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ABSTRACT: This study quantitatively analyzes fish community responses to environmental gradients in Myanmar's Irrawaddy Delta. Integrating beta-diversity partitioning, Threshold Indicator Taxa Analysis (TITAN), single-season occupancy modeling, and Structural Equation Modeling (SEM), and species co-occurrence network analysis, we identified primary environmental filters shaping ichthyofaunal structure. Spatial comparison between Bogale and Pyapon ecosystems revealed fundamentally distinct communities driven predominantly by species turnover (87.1%). Network topologies further demonstrated a significant spatial restructuring of biological interactions, with the primary network hub role shifting from the highly sensitive *Tenualosa ilisha* in the upper estuary to the highly adaptable *Macrognathus zebrinus* in the lower delta. Furthermore, SEM established a substantial structural connection between environmental stress and biological assemblage response ($\beta = 0.99$), suggesting water quality as the ecosystem's master driver. TITAN and occupancy models demonstrated an "estuarine enrichment" effect, where primary network hubs (*Tenualosa ilisha*, *Coilia neglecta*) reached peak occupancies only beyond high salinity thresholds (>18.16 ppt). However, escalating water temperatures act as a critical limiting factor, with a strict thermal boundary identified at 27.6 °C, beyond which sensitive taxa populations rapidly decline. These findings provide direct implications for adaptive fisheries management, underscoring the necessity of monitoring osmotic and thermal change-points to protect vital fisheries from compounded climate change impacts.

Keywords: Irrawaddy Delta; Ecological thresholds; Habitat squeeze; Salinity intrusion; Species turnover

1. Introduction

Tropical deltas are among the most biodiverse and productive ecosystems globally, providing essential ecosystem services and supporting the food security of millions through robust fisheries [1]. However, these systems are increasingly vulnerable to anthropogenic pressures and climate change. Specifically, salinity intrusion, driven by accelerated sea-level rise, shifting precipitation patterns, and upstream dam construction, is fundamentally altering the hydro-ecological characteristics of deltas worldwide [2]. The Irrawaddy Delta, one of Asia's largest and most ecologically significant deltaic systems, is currently facing such transitions. Yet, the specific impacts of these environmental shifts on its ichthyofaunal communities remain poorly understood [3].

Environmental parameters, including salinity, dissolved oxygen (DO), pH, and water temperature, act as primary filters for fish survival, recruitment, and spatial distribution [4]. In deltaic environments, increasing salinity levels often result in habitat squeeze for freshwater-dependent species while simultaneously creating novel niches for euryhaline or marine-migratory taxa [5]. Effectively managing these resources requires a quantitative understanding of species-specific responses and the identification of critical ecological thresholds-points where small changes in environmental drivers lead to abrupt shifts in occupancy or abundance [6].

The estuarine fish communities in the Irrawaddy Delta are highly diverse, encompassing a complex mix of both small- and large-bodied species. While many are resident species present year-round, the ecosystem also supports crucial migratory taxa, and these communities collectively form the backbone of local commercial fisheries. The study area spans two distinct ecosystems with contrasting habitat profiles: Bogale retains extensive, relatively intact mangrove forest areas, whereas Pyapon is predominantly characterized by modified landscapes, heavily dominated by agricultural lands, shrimp aquaculture ponds, and salt pans. Regarding fisheries management and spatial restrictions, Bogale hosts the strictly protected Meinmahla Kyun Wildlife Sanctuary, where all fishing activities are permanently banned. In the surrounding estuarine networks outside such sanctuaries, temporal restrictions—such as temporary fishing closures—are periodically enforced during critical spawning seasons to support stock replenishment.

This study investigates the environmental drivers shaping fish community dynamics in the Irrawaddy Delta across multiple ecological scales. The primary objectives are to evaluate the causal influence of physicochemical parameters on the estuarine community and to identify critical ecological change-points along key environmental gradients. By defining the habitat requirements and physiological thresholds of sensitive indicator species, this research aims to provide crucial scientific evidence to inform adaptive fisheries management and conservation strategies in the face of ongoing environmental change in the Irrawaddy Delta.

2. Materials and Methods

2.1. Study Area and Data Collection

Field sampling was conducted across 24 sites in the estuarine networks of Bogale and Pyapon Townships, Irrawaddy Delta. Sampling habitats were strategically selected and stratified across mangrove and agricultural areas based on the Forest Resources Assessment Map 2020 provided by the Forest Department, Myanmar (Figure 1) [7]. Fish occurrence and abundance were surveyed across three seasons in 2022 using a 400-m beach surrounding a gill net.

Concurrently, in situ water quality parameters (salinity, DO, water temperature, pH, and conductivity) were measured at each sampling site, specifically at peak high tide—the exact moment the net was secured onto the stakes—using specific portable meters (a CT 3080 salinity meter (Shenzhen Kedida Electronics Co., Ltd., Shenzhen, China) and a Sanxin portable water parameter measurer (Shanghai San-Xin Instrumentation, Inc., Shanghai, China)). This synchronization ensures that the recorded physicochemical variables accurately represent the environmental baseline during the primary period of fish activity and habitat utilization. Although fish assemblages were sampled year-round, predictive modeling utilized environmental data exclusively from the summer (dry) season. This targeted approach captures the period of highest baseline thermal and osmotic stress, representing the critical worst-case scenario for evaluating species vulnerability. The minimum linear distance between the mangrove and agricultural sampling sites was approximately 3.6 km. Given this close spatial proximity, the significant community differences observed between the two ecosystems are particularly noteworthy, especially when considering the varying mobility of the sampled species, which range from highly mobile migratory taxa to restricted resident species. Furthermore, taxonomic identification and valid nomenclature of all collected fish species were cross-verified according to FishBase (www.fishbase.org, accessed on 15 December 2025), Eschmeyer's Catalog of Fishes, and the Global Biodiversity Information Facility (GBIF).

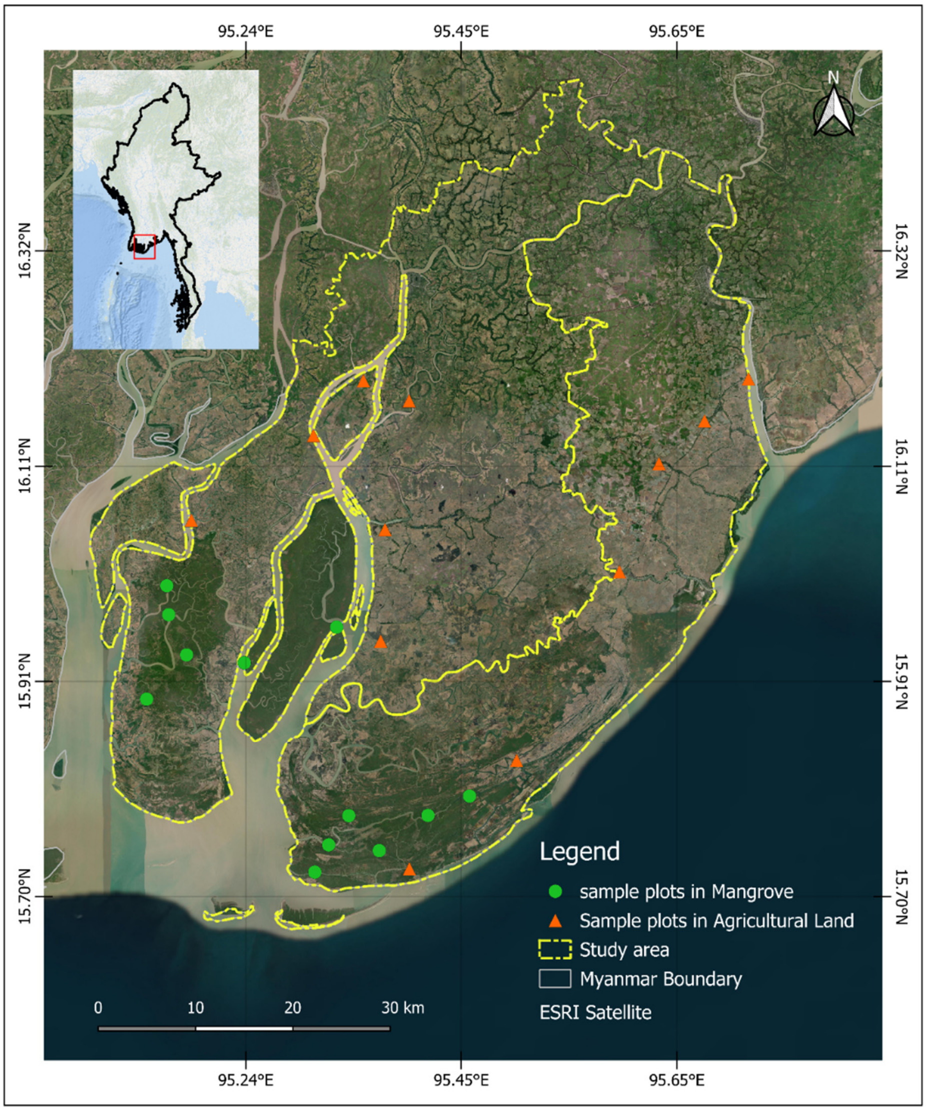

Figure 1. Map of the study area illustrating the 24 sampling sites within the estuarine networks of Bogale and Pyapon Townships in the Irrawaddy Delta, Myanmar. The sampling locations are strategically stratified across natural mangrove habitats and converted agricultural lands to capture spatial environmental heterogeneity.

While fish surveys were conducted across three seasons to comprehensively capture the annual species richness of the region, the baseline ecological conditions required for predictive modeling were specifically established using *in situ* physicochemical water parameters (salinity in ppt, dissolved oxygen, pH, and surface water temperature in °C) collected during the summer (dry) season. Utilizing the summer environmental parameters at each of the 24 sampling sites is critical for this vulnerability assessment, as it represents the period of highest baseline thermal and osmotic stress (worst-case scenario) against which the species' physiological tolerance limits must be buffered.

2.2. Beta Diversity Partitioning and Community Analysis

All statistical analyses were performed in R version 4.5.3 [8]. Spatial variation in fish community composition between Bogale and Pyapon townships was evaluated using a beta diversity partitioning framework. Total beta diversity (Sorensen dissimilarity) was decomposed into two distinct components: species turnover (Simpson dissimilarity), representing species replacement, and nestedness-resultant dissimilarity, representing species loss or gain in which one community is a subset of another [9]. Abundance data were converted into a binary presence-absence matrix to meet the requirements of the partitioning indices. The analysis was performed using the 'betapart' package [10] in R, enabling a clear distinction among the drivers of community differentiation.

Significant differences in community structure between the two study areas were tested through a Permutational Multivariate Analysis of Variance (PERMANOVA) using the 'adonis2' function in the 'vegan' package [11]. The test was executed with 999 permutations based on Bray-Curtis distances, which are functionally equivalent to the Sorensen index for presence-absence data. Community dissimilarity patterns were further visualized using Principal Coordinates Analysis (PCoA). All statistical plots and figures were generated using the 'ggplot2' package [12].

2.3. Structural Equation Modeling (SEM)

Structural Equation Modeling (SEM) was performed to analyze the complex interactions between physicochemical drivers and holistic fish community dynamics. A dual-latent variable framework was implemented to capture both the environmental pressures and the multifaceted biological responses [13]. The first latent construct, defined as 'Environmental Stress' (Env_Stress), was manifested through four physicochemical indicators: salinity, water temperature, pH, and dissolved oxygen (DO). The second latent construct, 'Assemblage Response', was measured using four key community metrics: Shannon-Wiener diversity, species composition, richness, and overall abundance. The structural model evaluated the direct causal influence of the environmental stress construct on the overall assemblage response. The analysis was implemented using the 'lavaan' package [14] in R. Maximum Likelihood (ML) estimation was used to derive standardized path coefficients (β and λ), allowing for a direct comparison of the effect sizes across varying measurement scales. The final hierarchical structure and causal pathways were visualized following LISREL conventions using the 'semPlot' package [13].

2.4. Community Thresholds and Multivariate Analysis (TITAN2 & CCA)

To identify ecological change-points and sensitive indicator taxa along environmental gradients, Threshold Indicator Taxa Analysis (TITAN) was employed [6]. This method facilitates the detection of synchronous changes in species distributions and frequency along physicochemical vectors. The analysis was performed using the 'TITAN2' package in R [15] with 500 bootstrap iterations to ensure the stability of identified thresholds. Taxa were categorized as indicators based on purity (≥0.90) and reliability (≥0.70) criteria, distinguishing between declining (z^-) and increasing (z^+) responders relative to each environmental driver.

Fish community responses to environmental gradients were examined through Canonical Correspondence Analysis (CCA) using the 'vegan' package [11,16]. The analysis focused on fish abundance data collected during the summer season, evaluated against four primary environmental parameters: salinity, pH, dissolved oxygen (DO), and water temperature. To improve the reliability of the ordination and reduce the influence of sporadic occurrences, rare species found in fewer than three sampling sites were excluded from the dataset. The statistical significance of the global CCA model and the individual environmental variables was assessed using ANOVA-like permutation tests with 999 permutations. This approach enabled the identification of specific environmental drivers that significantly influence species distribution. Community ordination and species-environment relationships were visualized via biplots generated with 'ggplot2' and 'ggrepel' [17].

2.5. Single-Season Occupancy Modeling

To estimate the probability of occupancy (ψ) while accounting for imperfect detection probability (p), a single-season occupancy modeling framework was implemented using the 'unmarked' package in R [18]. The analysis focused on the most sensitive and robust indicator species identified from the preceding TITAN analysis, ensuring that species-specific models represented the taxa most responsive to environmental shifts. Detection histories were constructed from replicate surveys. To satisfy the closure assumption of the occupancy framework, each of the 24 sampling sites was visited once per season across three distinct seasons in 2022, resulting in three replicate sampling occasions per site. To capture structural variations within the dynamic estuarine environment, surveys were strictly standardized based on local tidal cycles. The 400-m beach surrounding gill net was initially deployed and set along the substrate during low tide. At peak high tide, the net was secured onto fixed stakes to intercept fish assemblages. Biological specimens were subsequently collected as the water receded during the following ebb tide, ensuring a comprehensive inventory of the temporary estuarine inhabitants at each specific occasion. Environmental covariates (salinity, pH, DO, and water temperature) were standardized and incorporated into the models. Model selection was based on the Akaike Information Criterion (AIC), and predicted occupancy probabilities were visualized using ggplot2.

2.6. Species Co-Occurrence Network Analysis

Species co-occurrence networks were constructed to explore fish community interactions. Data formatting was conducted using the *tidyr* and *dplyr* packages [19]. Pairwise associations were evaluated via Spearman's rank correlations using the *Hmisc* package [20]. To ensure network robustness, only significant and strong correlations ($p < 0.05$, $|r| > 0.7$) were retained, and isolated species were excluded. Undirected, weighted networks were built with the *igraph* package [21]. Edge colors represented interaction types (blue for positive, red for negative), while edge widths scaled with correlation strength. Network hub species were identified based on the highest degree centrality. Network topologies were visualized using the Fruchterman-Reingold algorithm (3000 iterations) in R version 4.5.3 [8].

3. Results

3.1. Spatial Variation and Species Turnover

Spatial comparison of the fish communities between Bogale and Pyapon mangrove ecosystems revealed highly significant differences in species composition (PERMANOVA, $p = 0.001$). The total beta diversity between the two townships was 0.817. In beta diversity indices, values closer to 1 indicate high dissimilarity. Partitioning to this total beta diversity demonstrated that species turnover accounted for much of the dissimilarity (0.711, representing 87.1% of the total beta diversity), whereas the nestedness-resultant fraction was relatively minor (0.105) (Figure 2). This exceptionally high turnover value indicates that the dissimilarity between the two townships is not due to species loss or degradation in one area but rather driven by the spatial replacement of unique fish species. As subsequently supported by our Canonical Correspondence Analysis (CCA), this spatial replacement directly reflects distinct environmental adaptations, with species distributions strongly constrained by primary physicochemical filters such as salinity and dissolved oxygen across the estuarine networks.

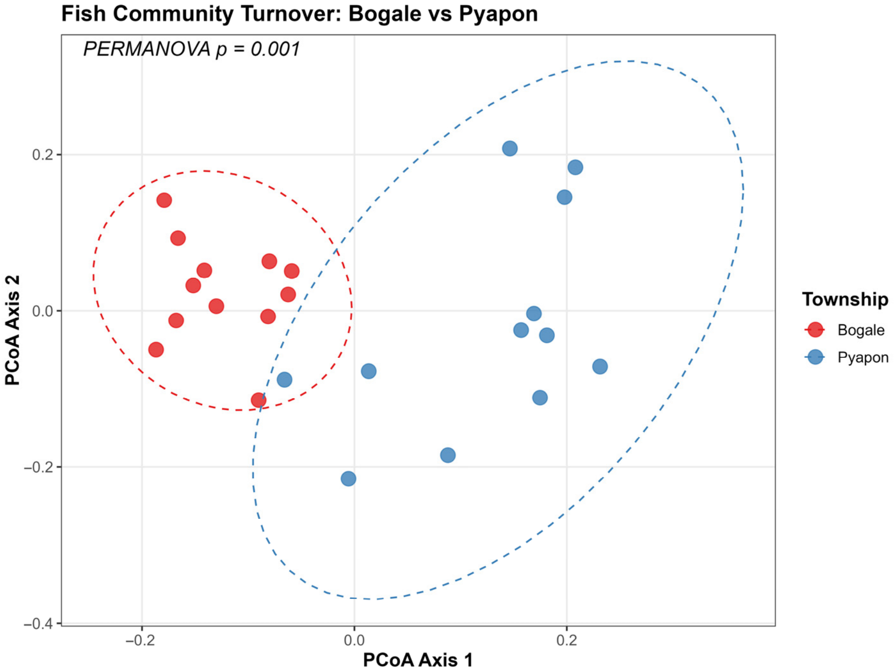

Figure 2. Principal Coordinates Analysis (PCoA) plot of fish community turnover between Bogale (red) and Pyapon (blue) ecosystems. Dashed lines indicate 95% confidence ellipses. The distinct spatial separation is highly significant (PERMANOVA, $p = 0.001$), driven primarily by a high rate of species turnover (87.1%).

3.2. Environmental Drivers of Community Assemblage (SEM)

The dual-latent Structural Equation Model (SEM) revealed a significant, near-perfect standardized relationship ($\beta = 0.99$) between the latent environmental stress construct and the overarching fish assemblage response (Figure 3). The ‘Environmental Stress’ construct was predominantly driven by water temperature ($\lambda = -0.89$) and salinity ($\lambda = 0.74$), with substantial positive contributions from DO ($\lambda = 0.70$) and pH ($\lambda = 0.47$). This indicates that thermal gradients and salinity intrusion are the primary factors defining the environmental condition in the delta.

On the biological side, the ‘Assemblage Response’ construct was robustly represented by species composition ($\lambda = 1.00$) and richness ($\lambda = 0.78$), followed by total abundance ($\lambda = 0.77$) and diversity ($\lambda = 0.68$). Although the extraordinarily high effect size ($\beta = 0.99$) strongly implies that physicochemical shifts comprehensively dictate community structure, the direct structural path did not reach formal statistical significance ($p > 0.05$). This is likely attributable to the analytical constraints of fitting a highly complex dual-latent framework to a limited spatial sampling size. Nonetheless, the substantial indicator loadings indicate that compositional turnover and species richness are highly sensitive to combined thermal and osmotic stresses. Detailed model diagnostics are as follows: CFI = 0.92, TLI = 0.84, RMSEA = 0.27, and SRMR = 0.11. While the CFI indicates an acceptable model fit, the other indices reflect the expected statistical constraints of fitting a parameterized structural model to a restricted spatial sample size ($n = 24$).

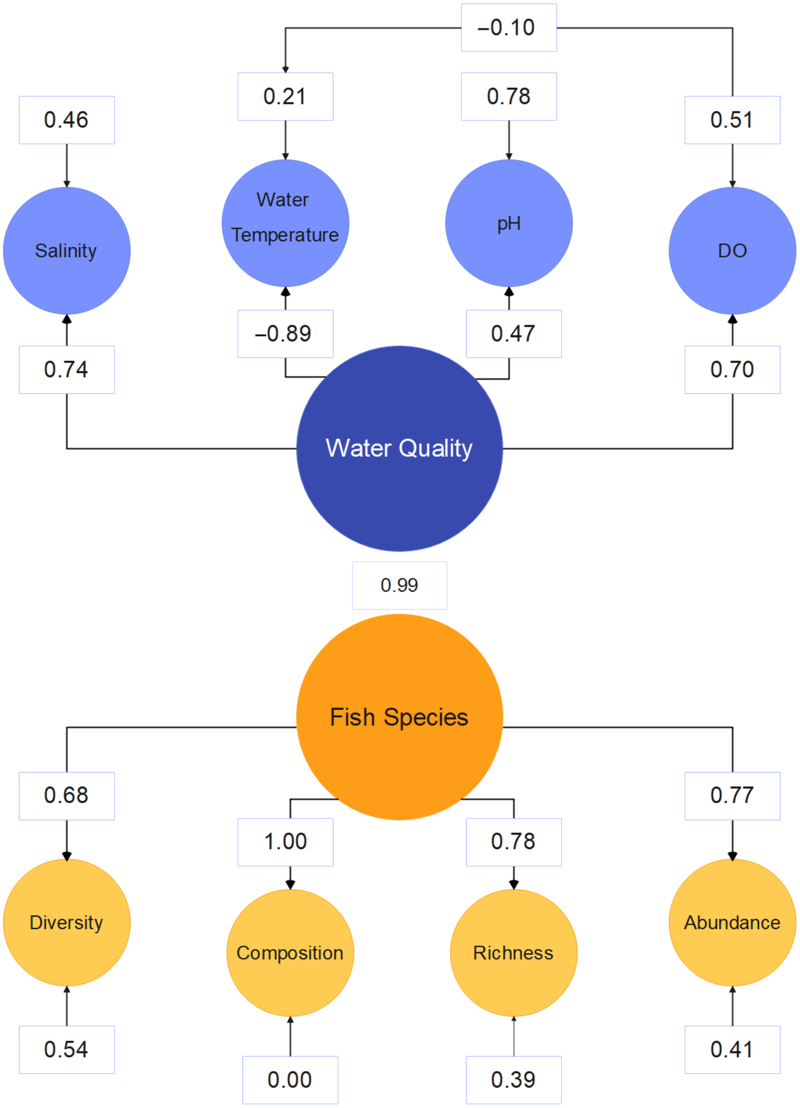

Figure 3. Structural Equation Model (SEM) illustrates the interactions between the latent "Env_Stress" construct and the biological "Assemblage Response" construct in the Irrawaddy Delta. Values on the paths represent standardized coefficients (β and λ). The model demonstrates a substantial effect size ($\beta = 0.99$) connecting environmental drivers to fish community metrics, where water temperature ($\lambda = -0.89$) and species composition ($\lambda = 1.00$) serve as the strongest respective indicators.

3.3. Community Thresholds and Niche Associations (TITAN2 & CCA)

The TITAN2 analysis identified distinct community-level change-points across the environmental gradients (Figure 4). Notably, all significant indicator species for salinity exhibited positive (z^+) responses, indicating a strong estuarine and marine enrichment effect. Top indicators species, including *Coilia neglecta* (Whitehead, 1867), *Tenualosa ilisha* (Hamilton, 1822), and *Sillaginopsis domina* (Cuvier, 1816), demonstrated sharp increases in occurrence beyond high-salinity thresholds of 19.18 ppt, 18.16 ppt, and 18.16 ppt, respectively. Conversely, water temperature acted as a critical limiting factor; a community transition point was identified at 27.6 °C, driven primarily by network hub species such as *T. ilisha*. Other sensitive declining (z^-) indicators, including *Coilia dussumieri* Valenciennes, 1848, and *Salmostoma sardinella* (Valenciennes, 1844), also showed sharp reductions in occurrence as temperatures escalated towards 28.2 °C and 28.8 °C, respectively. Furthermore, dissolved oxygen (DO) and pH demonstrated distinct threshold effects. DO levels below 5.64 mg/L triggered the decline (z^-) of sensitive species such as *Moolgarda tade* (Fabricius, 1775) and *Notopterus notopterus* (Pallas, 1769), whereas estuarine taxa like *T. ilisha* showed increasing frequencies as DO improved beyond 6.00 mg/L. Along the pH gradient, a synchronized positive transition occurred, with *T. ilisha* and *S. domina* both exhibiting sharp increases beyond a pH threshold of 7.93.

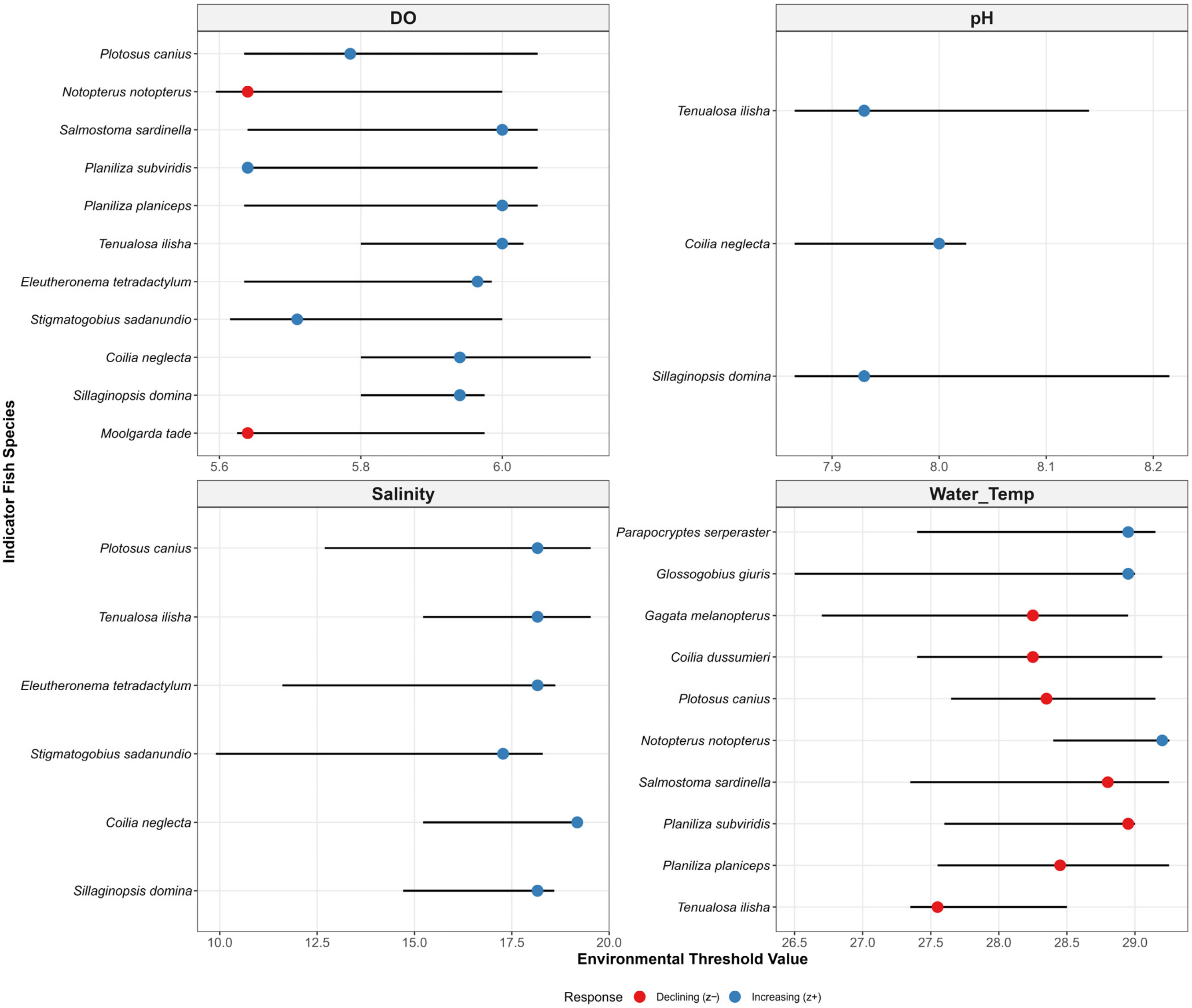

Figure 4. Threshold Indicator Taxa Analysis (TITAN) plots illustrating the change-points for significant fish species along four environmental gradients (Salinity, pH, DO, and Water Temperature). Colored dots represent the individual species change-points (ienv.cp), with red indicating declining (z^{-}) and blue indicating increasing (z^{+}) responses. Horizontal black lines denote the 5th and 95th percentiles of the bootstrap distribution. Species are filtered based on purity (≥0.90) and reliability (≥0.70).

Canonical Correspondence Analysis (CCA) further corroborated these findings, revealing that *T. ilisha*, *C. neglecta*, and *S. domina* were strongly associated with the salinity vector, reflecting their preference for higher salinity environments within the estuarine gradient (Figure 5). The ordination further elucidated the specific niche associations of the indicator species identified via TITAN2. The ordination revealed distinct clustering along environmental gradients, with the first two axes explaining 32.71% of the total community variation (CCA1: 26.86%; CCA2: 5.85%) (Figure 5). Salinity, DO, and pH were identified as highly influential vectors driving the community structure along the first axis. Target estuarine species, particularly *T. ilisha*, *C. neglecta*, and *S. domina*, exhibited strong associations with these parameters, clustering distinctly along the environmental gradients. Conversely, species such as *M. tade* and *N. notopterus* were positioned in the opposite end of the ordination space, indicating a stronger association with water temperature. This spatial ordination clearly reflects the transition in community composition governed by physicochemical filtering in the estuarine habitat.

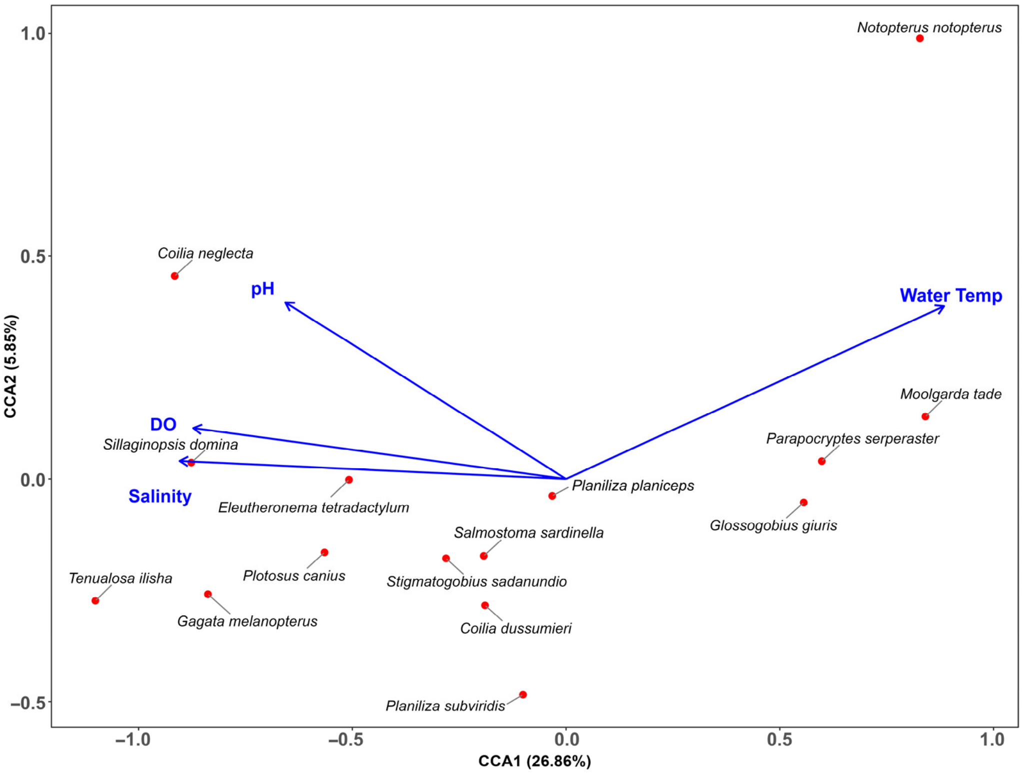

Figure 5. Canonical Correspondence Analysis (CCA) ordination biplot showing the relationship between TITAN2-derived indicator species and key environmental variables. The first two axes explain 26.86% and 5.85% of the variance, respectively. Blue vectors represent the direction and strength of environmental gradients (Salinity, pH, Water Temp, and DO), while red dots indicate the ordination of individual species in the environmental space.

3.4. Species-Specific Occupancy Responses

Single-season occupancy models revealed distinct niche-response patterns that aligned perfectly with the community-level TITAN2 thresholds (Figure 6). Contrary to initial hypotheses of freshwater affinity, all modeled target species demonstrated a strong preference for high-salinity zones. Specifically, *C. neglecta*, *T. ilisha*, *S. domina*, and *Plotosus canius* Hamilton, 1822 exhibited steeply positive occupancy trends, with their probabilities of occurrence peaking significantly only after crossing their respective high-salinity thresholds (>18.16 ppt). While these species adapt well to increasing salinity, they displayed a consistent and sharp negative response to water temperature, with occupancy probabilities dropping drastically as temperatures exceeded the 27.6 °C threshold.

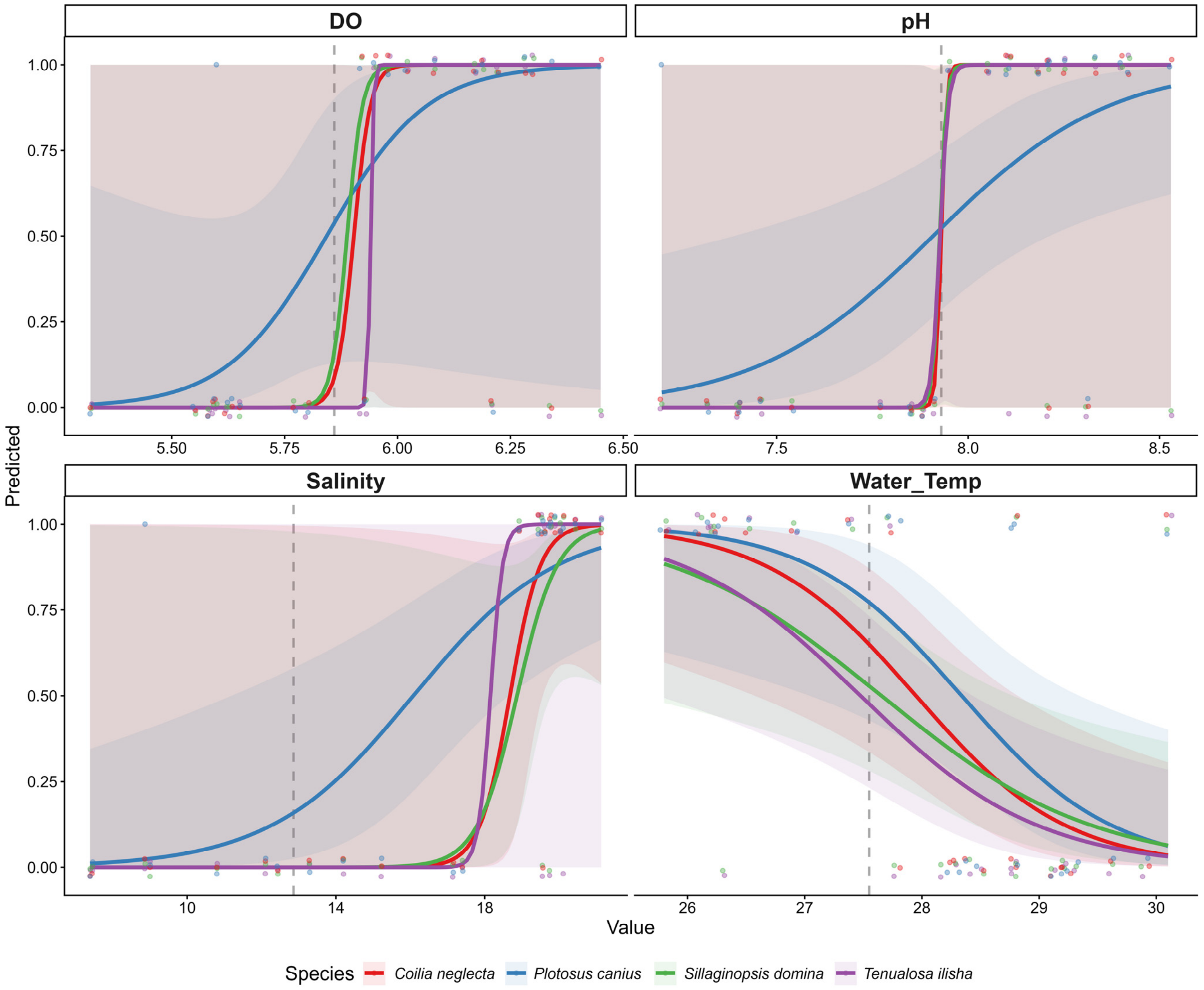

Figure 6. Predicted occupancy probability (ψ) of four key fish species relative to environmental gradients in the Irrawaddy Delta. Solid lines represent the mean occupancy estimates, with shaded areas indicating 95% confidence intervals. The colored dots (rug plot) represent original presence (top) and absence (bottom) data. Vertical dashed lines denote the ecological change-points (ienv.cp) identified via TITAN2 analysis, illustrating the alignment between species-specific responses and community-level transitions.

3.5. Species Co-Occurrence Networks and Network Hubs

To elucidate complex interspecific associations and identify ecologically critical taxa within the distinct estuarine habitats, abundance-based Spearman rank correlation networks were constructed for Bogale and Pyapon townships ($|r| > 0.7$, $p < 0.05$). The network topologies revealed a significant spatial restructuring of fish community interactions and a complete shift in network hubs between the two ecosystems (Figure 7A,B).

In the Bogale mangrove ecosystem, the co-occurrence network was predominantly anchored by anadromous and estuarine-affiliated taxa (Figure 7A). Network centrality analysis identified *T. ilisha* as the primary network hub (degree = 10), followed closely by *Johnius belangerii* (Cuvier, 1830) (degree = 9), *S. domina* (degree = 7), and *Planiliza planiceps* (Valenciennes, 1836) (degree = 7). These central hub species exhibited strong positive associations (blue edges) with each other, forming a tightly knit core module that reflects shared niche preferences within the localized environmental conditions.

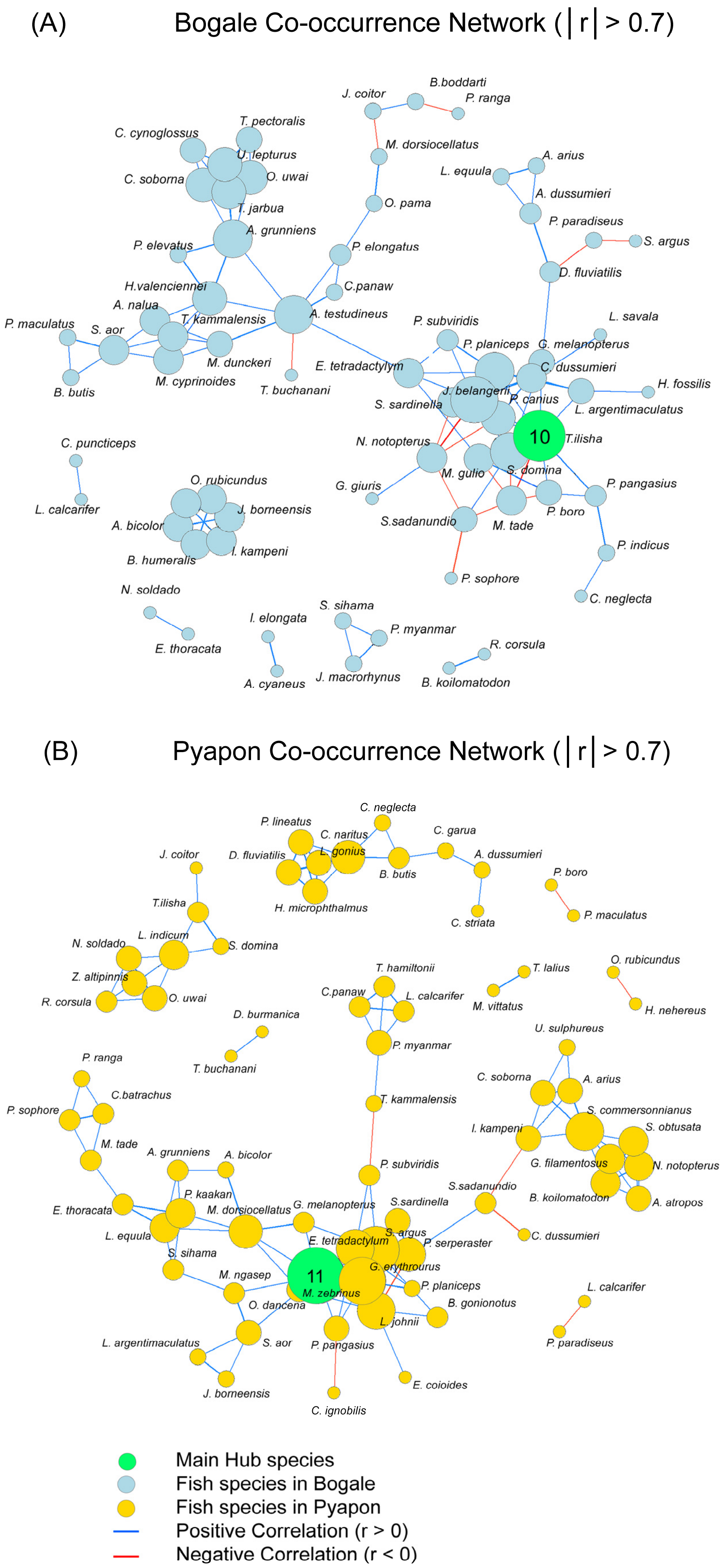

Figure 7. Species co-occurrence networks illustrating interspecific associations within the estuarine fish communities. (**A**) The network topology in the Bogale ecosystem, anchored primarily by *T. ilisha*. (**B**) The reorganized network structure in the Pyapon ecosystem, dominated by *M. zebrinus*. Nodes represent individual fish species, with sizes scaled proportionally to their degree

of connectivity (indicating high connectivity). Edges denote statistically significant Spearman rank correlations ($|r| > 0.7$, $p < 0.05$). Blue lines indicate positive co-occurrence (shared habitat preferences), whereas red lines indicate negative associations (mutual exclusion).

Conversely, the Pyapon network demonstrated a complete compositional shift in its foundational structure (Figure 7B). The primary network hub role was unexpectedly overtaken by *Macrognathus zebrinus* (Blyth, 1858). Although traditionally classified as a freshwater-associated species, its identity was verified through voucher specimens, and it exhibited the highest connectivity (degree = 11) within the more saline Pyapon network. This species was supported by a different suite of highly connected taxa, including *Scatophagus argus* (Linnaeus, 1766) (degree = 9), *Gerres erythrourus* (Bloch, 1791) (degree = 9), and *Eleutheronema tetradactylum* (Shaw, 1804) (degree = 7). The displacement of *T. ilisha* and *S. domina* from the primary hub positions in Pyapon highlights a substantial restructuring of the original community network and its subsequent reorganization. Furthermore, the presence of distinct negative associations (red edges) in both networks signifies mutual exclusion among certain species, likely driven by varying tolerances to the primary environmental filters such as salinity gradients across the delta.

4. Discussion

4.1. Spatial Variation and Habitat Heterogeneity

Beta diversity partitioning revealed that the fish communities in Bogale and Pyapon are fundamentally distinct. The total beta diversity (0.817) was driven predominantly by species turnover (87.1%) rather than nestedness (Figure 2).

This exceptionally high rate of species replacement is not only driven by osmotic gradients but is also heavily influenced by the stark contrast in physical habitat structure between the two townships. Bogale retains extensive and relatively intact mangrove ecosystems, providing critical structural complexity, detritus-based food webs, and nursery grounds that support estuarine-dependent taxa [22]. Conversely, mangrove cover in Pyapon is severely degraded or nearly non-existent, having been largely replaced by agricultural lands or open coastal zones [7]. The loss of this vital biogenic habitat acts as a primary environmental filter, compounding the effects of salinity intrusion and driving the spatial replacement of species.

Consequently, effective conservation strategies must prioritize the protection of multiple distinct mangrove habitats across different townships. Because communities replace one another rather than merely degrading into subsets, preserving a single protected area cannot serve as an adequate surrogate for maintaining the entire delta’s biodiversity [23].

4.2. Salinity as a Driver of Estuarine Enrichment

Integrated analytical frameworks demonstrate that salinity intrusion in the Irrawaddy Delta acts as a catalyst for “estuarine enrichment” rather than a mere displacement mechanism. Threshold indicator taxa analysis (TITAN) and single-season occupancy modeling provide definitive evidence that key economically significant species, specifically *T. ilisha*, *C. neglecta*, and *S. domina*, exhibit strong reliance on elevated salinity gradients (Figures 4 and 6). These specialized taxa experience a community-level transition and reach their peak occupancy probabilities only beyond the high-salinity concentrations of 18.16 to 19.18 ppt. This spatial pattern suggests that the inland penetration of marine waters is actively expanding the available niche space for marine-migratory and euryhaline species. Such a trajectory facilitates a fundamental restructuring of the ichthyofaunal community, transitioning it toward an increasingly marine-dominated assemblage [22,24]. This expansion reflects typical deltaic dynamics, in which salinity-driven habitat modifications create novel ecological opportunities for estuarine-affiliated populations [5,25]. This landward expansion of the salinity gradient effectively optimizes the availability of structural niches for brackish-water- and marine-tolerant species, such as *T. ilisha* and *C. neglecta*, thereby facilitating estuarine enrichment. However, from a macro-ecological perspective, this environmental shift creates a distinct dichotomy of ecological ‘winners and losers’ within the deltaic network. While marine-tolerant taxa (the winners) expand their spatial boundaries and capitalize on newly salinized habitats, strictly freshwater stenohaline species (the losers)—such as *N. notopterus*—suffer from severe habitat contraction and localized displacement. This structural asymmetric reorganization highlights that salinity intrusion does not merely change species richness but fundamentally alters the baseline community composition by filtering out salt-sensitive freshwater specialists and replacing them with resilient estuarine generalists.

4.3. Thermal Limits and the Habitat Squeeze

Although salinity intrusion facilitates the landward expansion of euryhaline taxa, integrated structural equation modeling and threshold analyses elucidate a complex mechanistic pathway driven by climatic shifts. The SEM revealed an exceptionally high standardized path coefficient ($\beta = 0.99$) between environmental stress and the biological assemblage response. However, it is important to note that this path did not reach formal statistical significance ($p > 0.05$), likely due to sample size constraints inherent in fitting a highly parameterized model to 24 sites. Therefore, we present this large effect size as a compelling but preliminary result that warrants further investigation with a larger dataset. Nonetheless, ecologically, this strong preliminary relationship suggests that the delta’s ichthyofaunal community is highly sensitive to physicochemical fluctuations. Because the community appears tightly coupled to these environmental drivers, particularly temperature and salinity, any drastic climate-induced shifts could trigger rapid and severe restructuring of the fish assemblage, exacerbating the habitat squeeze. Structural equation modeling (SEM) reveals a significant negative interaction between water temperature and dissolved oxygen (standardized coefficient = −0.10) (Figure 3), a dynamic of critical concern in rapidly warming deltaic systems where oxygen solubility is inherently compromised by thermal gain [26]. Notably, threshold indicator taxa analysis (TITAN) identifies a critical thermal boundary at 27.6 °C (Figure 4). Beyond this tipping point, network hub species such as *T. ilisha* exhibit rapid declines in occupancy, suggesting that these populations are operating near their upper physiological limits. Consequently, the local ichthyofauna encounters a unique environmental “habitat squeeze”: while marine-affiliated species are drawn further inland by expanding salinity niches, the warming of shallow waters in these upper-estuarine reaches presents a severe physiological barrier. Such synergistic stressors, salinity intrusion compounded by lethal thermal limits and subsequent hypoxia, underscore the acute vulnerability of the Irrawaddy Delta’s biodiversity to shifting global climate regimes [1,2].

4.4. Co-Occurrence Network Restructuring and Network Hub Taxa Shifts

Species co-occurrence networks provide critical insights into the functional organization and stability of ecological communities beyond simple diversity metrics [27]. The topological comparison between the Bogale and Pyapon ecosystems revealed a significant spatial restructuring of interspecific associations (Figure 7A,B). This complete reorganization of network modules perfectly corroborates the beta diversity findings, where spatial dissimilarity was driven predominantly by an exceptionally high species turnover rate (87.1%). Ecologically, this indicates that environmental gradients do not merely cause a nested loss of species; rather, the entire interaction web is dismantled and replaced by a novel community structure [9,22].

In the Bogale ecosystem, network centrality metrics identified *T. ilisha* as the primary network hub, closely supported by other estuarine hubs, such as *J. belangerii*, *S. domina*, and *P. planiceps* (Figure 7A) [28]. This highly connected network reflects the supportive capacity of Bogale’s intact mangrove habitats. However, as previously established by TITAN2 and single-season occupancy models, the spatial distribution of this specific network hubs taxon is strictly governed by critical physicochemical thresholds, heavily relying on specific salinity and temperature optimal ranges.

As primary environmental filters, specifically escalating salinity and the severe physical loss of mangrove vegetation, intensify towards the lower estuarine reaches of Pyapon, the foundational structure of the community shifts considerably. The primary network hub's role is overtaken by resilient taxa, notably *M. zebrinus* and *S. argus* (Figure 7B). Ecologically, such topological shifts indicate that the combined degradation of mangrove habitats and osmotic stress do not merely displace individual species but actively dismantle and restructure entire biological interaction networks [22,24]. Consequently, the loss or spatial displacement of core network hub species like *T. ilisha* due to environmental shifts could trigger cascading secondary impacts, fundamentally altering energy flow and potentially impacting the stability of traditional fishery networks in the Irrawaddy Delta.

An unexpected observation within the spatial network restructuring in Pyapon is the high connectivity of *M. zebrinus* as a primary network hub. Traditionally recognized as a strictly freshwater spiny eel (Mastacembelidae), its confirmed identity—verified through rigorous morphological examination of voucher specimens—and its prevalence in the more saline lower delta suggest a potential degree of ecological plasticity. In fact, our broader field survey observations indicate that this species is frequently encountered across lowland areas in Irrawaddy, Sittang, Salween, and Tanintharyi drainages in Myanmar, highlighting its widespread adaptability. However, we explicitly note that suggesting true euryhaline adaptation remains a hypothesis based primarily on our co-occurrence and abundance data. An equally plausible explanation is that these individuals were utilizing localized freshwater or oligohaline microhabitats (e.g., agricultural drainage channels or canal mouths) within the broader Pyapon estuarine landscape. Future direct physiological testing or fine-scale, site-specific salinity profiling is required to definitively confirm their true physiological tolerance to elevated estuarine salinity. While the broader community shift in Pyapon is primarily characterized by an influx of marine-migratory species, the presence of *M. zebrinus* indicates that certain native freshwater taxa may possess the euryhaline capacity to tolerate intensifying osmotic gradients. Grouping such adaptable taxa merely as "marine-tolerant" likely overlooks their specific physiological resilience. This transition hypothesizes that salinity intrusion may not only facilitate marine species expansion but also inadvertently select for highly adaptable native species capable of persisting under altered physicochemical stress.

4.5. Study Limitations and Future Directions

Despite the comprehensive multi-scale insights provided by this study, certain methodological limitations must be acknowledged. First, the spatial sampling framework was constrained to 24 distinct monitoring sites. While these sites effectively capture the primary ecological gradients of the Ayeyarwady Delta, applying data-intensive frameworks such as Threshold Indicator Taxa Analysis (TITAN2) and Structural Equation Modeling (SEM) within this relatively small sample size may inherently reduce overall statistical power and elevate the risk of model over-fitting. Consequently, the inferred ecological thresholds and causal pathways should be interpreted with caution. Second, a notable temporal discrepancy exists within our dataset: although ichthyofaunal assemblages were systematically monitored across three distinct seasons to evaluate temporal dynamics, the physicochemical water quality variables utilized in the environmental models were primarily restricted to a single representative season. This asymmetry introduces potential seasonal bias, as it may overlook fine-scale temporal fluctuations in environmental drivers—such as shifting salinity wedges during the monsoon. Future research should expand both the spatial grid and standardize concurrent environmental sampling across all seasons to validate the robustness of these ecological networks and thresholds.

5. Conclusions

In summary, this multi-scale assessment reveals that the ichthyofaunal community of the Irrawaddy Delta is undergoing a substantial structural shift driven by interacting environmental stressors. Rather than causing a simple decline in regional biodiversity, salinity intrusion actively facilitates an estuarine enrichment effect, expanding the inland niche space for marine-migratory and euryhaline taxa. However, this landward expansion is fundamentally constrained by critical thermal boundaries. As global climate change accelerates, the synergistic pressures of warming shallow waters and altering osmotic gradients will likely subject these fish assemblages to a severe physiological habitat squeeze. Furthermore, topological shifts in species co-occurrence networks indicate that these physicochemical filters do not merely displace individual species but actively dismantle and restructure entire biological interaction networks. The spatial displacement of core network hubs species, such as *T. ilisha*, highlights the severe risk of cascading secondary impacts that could potentially lead to the collapse of traditional fishery networks. Consequently, future conservation and fisheries management frameworks in Myanmar must transition from traditional flow-centric approaches towards adaptive strategies. Prioritizing the continuous monitoring of these critical physicochemical tipping points will be essential to safeguarding the resilience of the delta's vital fisheries against compounded climatic impacts.

Supplementary Materials

The following supporting information can be found at: https://www.sciepublish.com/article/pii/1098.

Statement of the Use of Generative AI and AI-Assisted Technologies in the Writing Process

During the preparation of this work, the author(s) used SciAIEngine (Scientific AI Engine) (https://sciai.las.ac.cn/) developed by the National Science Library of CAS in order to improve language readability and clarity. After using these tools/services, the author(s) reviewed and edited the content as needed and take full responsibility for the content of the published article.

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Author Contributions

Conceptualization, X.C.; Methodology, X.C.; Formal Analysis, K.K.T.T. and T.H.; Investigation, K.K.T.T., H.N.N., T.N.O. and X.C.; Resources, T.N.O.; Data Curation, K.K.T.T., T.H., T.Q., J.B., J.L. and H.Z.P.; Writing—Original Draft Preparation, K.K.T.T. and C.L.; Writing—Review & Editing, X.C.; Supervision, X.C.; Funding Acquisition, X.C.

Ethics Statement

Ethical review and approval were waived for this study, as the methodology was restricted to standard ecological biodiversity surveys. Fish were captured using traditional surrounding nets strictly for taxonomic identification and abundance recording. The study did not involve any invasive physiological experiments, pharmacological interventions, or the targeted manipulation of endangered species. This research was conducted in accordance with the animal care and use guidelines of Kunming Institute of Zoology, Freshwater Fisheries Law Myanmar, 1991 and the Conservation of Biodiversity and Protected Areas Law, Myanmar (2018).

Informed Consent Statement

Not applicable.

Data Availability Statement

The original raw datasets and R scripts supporting the conclusions of this article are included within the article and its Supplementary Materials. Further inquiries can be directed to the corresponding author.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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