Environmental cues driving intra-reservoir and directional migration of *Macrobrachium rosenbergii*: Insights from a culture-based fishery in Sri Lanka

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Abstract: The culture-based fishery (CBF) for giant freshwater prawn (*Macrobrachium rosenbergii*) is increasingly important in Sri Lankan reservoirs, yet the spatial ecology of stocked populations remains critically understudied. This study examined spatial segregation and directional migration cues of *M. rosenbergii* in the Hurulu Wewa reservoir between June 2020 and April 2021. The reservoir was stratified into three hydrological zones: lacustrine (deep), transitional and upstream lotic (shallow). Monthly sex-specific catch data were analysed alongside rainfall, outflow, depth and storage capacity using generalised additive models (GAMs). Sex ratios differed significantly among strata ($p = 0.011$), with pronounced male bias in upstream and transitional zones compared to the lacustrine zone. This spatial structuring persisted monthly ($p = 0.429$), indicating stable habitat segregation. GAMs revealed strong non-linear associations between depth, storage capacity and prawn distribution, with rainfall–outflow interactions influencing hydrological gradients. Increased male aggregation in upstream zones during hydrological transitions suggests flow-mediated directional movement. We conclude that hydrological gradients serve as primary ecological cues structuring *M. rosenbergii* distribution in CBF systems. These findings provide the first quantitative evidence of directional migration cues for this species in reservoirs and support stratum-specific stocking and harvest strategies to enhance fishery sustainability.

Keywords: Giant freshwater prawn, Inland fisheries, Reservoirs, Spatial structure

INTRODUCTION

Reservoir fisheries in Sri Lanka make a substantial contribution to rural livelihoods, nutritional security and local market economies. In inland dry-zone districts where alternative protein sources may be limited or economically inaccessible, inland fish production represents a critical dietary component (De Silva, 1988; Amarasinghe *et al.*, 2022). Also, culture-based fisheries (CBFs) have emerged as a cost-effective and community-centered enhancement strategy, augmenting natural productivity through managed stocking while maintaining the ecological integrity of open water systems (Amarasinghe and Nguyen, 2010). The integration of this stocking-based enhancement into these lentic systems capitalises on underutilised trophic niches, seasonal productivity pulses and relatively low input requirements. Unlike intensive aquaculture, CBF operates within the ecological carrying capacity of reservoirs, relying on natural food webs and hydrological regimes (Moreau *et al.*, 2000; Amarasinghe *et al.*, 2014;). Within this context, the giant freshwater prawn (GFP) – *Macrobrachium rosenbergii*, has gained prominence as a high-value candidate species for stocking in reservoirs.

The GFP combines several biological and economic attributes that align well with CBF objectives. It commands premium market prices due to strong domestic and export demand, exhibits rapid somatic growth under favourable conditions and demonstrates compatibility with polyculture systems that include finfish species (Chandrasoma *et al.*, 2015; Pushpalatha *et al.*, 2017). Its omnivorous feeding ecology enables effective utilisation of benthic detritus, periphyton and macroinvertebrates (New, 1976), thereby reducing direct competition with pelagic fish species. Furthermore, hatchery technologies in Sri Lanka have advanced to reliably produce post-larvae (PL), typically up to PL15 stage, enabling controlled seed supply for reservoir enhancement programmes (Asoka and Hettiarachchi, 2004; Pushpalatha and Chandrasoma, 2010).

Notwithstanding its production advantages, *M. rosenbergii* is characterized by complex behavioural ecology and pronounced sexual dimorphism which may significantly influence its performance in large, heterogeneous water bodies. Male prawns exhibit hierarchical polymorphism, typically classified into distinct morphotypes, small males, orange-clawed males and dominant blue-clawed males each associated with differential growth rates, aggression levels and territorial dominance (Karplus, 2005; Ráanan *et al.*, 1991). Larger males often monopolise favourable microhabitats, particularly shallow zones with structured substrates that facilitate shelter and mate guarding. In contrast, females generally exhibit less aggressive behaviour and may preferentially occupy deeper or more hydrologically stable environments (Peebles, 1979; New *et al.*, 2009; Malecha, 2012). Such behavioural divergence suggests the possibility of sex-specific spatial segregation within expansive reservoir systems.

In natural riverine environments, GFP exhibits amphidromous life-history characteristics. Spawning occurs in freshwater; however, larval development requires brackish conditions, typically found in estuaries or coastal lagoons where salinity gradients trigger successful metamorphosis (Chand *et al.*, 2015; Hosain *et al.*, 2021). Females carrying fertilised eggs undertake downstream migrations toward saline waters, a movement believed to be regulated by endogenous circadian and circadian rhythms interacting with environmental cues such as flow velocity and salinity gradients (Wei *et al.*, 2021). Larvae subsequently migrate upstream as post-larvae, completing the life cycle. This bidirectional migratory instinct reflects a finely tuned evolutionary adaptation to river–estuary continua.

Aquaculture practices have deliberately interrupted this natural cycle for production efficiency. In hatchery systems, larval stages are reared under controlled brackish conditions until metamorphosis to post-larvae, after which juveniles are acclimated to freshwater and stocked into grow-out systems, including reservoirs (Malecha *et al.*, 1980, 1981). In culture-based fisheries, individuals spend their early ontogenetic stages in artificial environments and subsequently complete growth and maturation entirely within freshwater impoundments. The reproductive cycle may proceed physiologically within reservoirs, and opportunities for downstream migration to saline environments are typically absent due to embankments, sluice gates and spill structures that disrupt longitudinal connectivity.

The impounded nature of reservoirs thus creates an ecological paradox. On one hand, embankments and water-control structures restrict natural migratory pathways; on the other, irrigation-driven outflows and spill events generate artificial flow gradients that may simulate rheotactic stimuli (Lee and Fielder, 1984). Flow pulses during irrigation releases can produce directional currents, particularly along the longitudinal axis from riverine inflow zones toward the dam. If females retain an intrinsic downstream migratory tendency linked to reproductive conditioning, such hydrological gradients could potentially stimulate movement toward deeper lacustrine zones adjacent to sluice gates and spillways. Conversely, dominant males, exhibiting territorial and substrate-associated behaviour, may preferentially remain in shallow upstream or transitional areas where structural complexity enhances competitive advantage.

Reservoirs are not homogeneous lentic basins, but exhibit pronounced longitudinal zonation. The upstream riverine (lotic) zone is generally shallow, turbid and influenced by inflow dynamics, characterised by higher nutrient inputs and variable dissolved oxygen regimes (Thornton *et al.*, 1990). The transitional zone represents an intermediate hydrodynamic environment where sedimentation increases and flow velocity decreases. Near the dam embankment lies the lacustrine zone, typically deeper, clearer and more thermally stratified, with distinct benthic substrates and altered trophic pathways (Thornton *et al.*, 1990). Such spatial heterogeneity influences primary productivity, benthic macroinvertebrate assemblages and shelter availability—factors directly relevant to prawn habitat selection. Differences in depth profiles, turbidity gradients, dissolved oxygen dynamics and food availability collectively generate ecological niches that may structure intra-reservoir distribution.

Despite expanding interest in production metrics, such as growth performance, yield optimisation and economic returns, behavioural ecology within large reservoir systems remains comparatively understudied.

Understanding these dynamics is critical for optimising the CBF performance of GFP. If females exhibit downstream-oriented tendencies during maturation, disproportionate accumulation near dam structures could increase vulnerability to escapement through spillways during overflow events, thereby reducing harvestable biomass. Hydrological manipulations associated with irrigation scheduling could unintentionally shape distribution patterns, influencing catch per unit effort across reservoir strata. Without robust ecological insight, management interventions risk overlooking behavioural processes that mediate production outcomes.

Moreover, climate variability and increasingly unpredictable rainfall regimes in Sri Lanka may intensify hydrological fluctuations, altering flow pulses and water-level dynamics (Jayasinghe *et al.*, 2005; Nadarajah *et al.*, 2019). These changes could amplify or dampen potential migration cues, further complicating spatial ecology within reservoirs. A mechanistic understanding of how hydrology interacts with intrinsic behavioural rhythms is therefore essential not only for yield optimisation but also for adaptive management under changing environmental conditions.

Against this backdrop, the present study was designed to address critical knowledge gaps concerning the spatial ecology of *M. rosenbergii* in culture-based fisheries in reservoir systems. Specifically, it aimed to quantify spatial and temporal variation in prawn abundance across distinct longitudinal zones; examine sex ratio differences among reservoir strata; model hydrological interactions influencing habitat dynamics; and interpret potential migration cues linking water-flow gradients with observed distribution patterns. We hypothesised that *M. rosenbergii* exhibits significant, stable spatial segregation across reservoir strata. By integrating ecological theory with applied fisheries management, this research seeks to elucidate how evolutionary behavioural traits operate within anthropogenically modified freshwater systems. Such insights are expected to contribute to more refined stocking strategies, improved harvest planning and enhanced sustainability of CBF within Sri Lanka's historically engineered yet ecologically dynamic dry-zone reservoirs.

MATERIALS AND METHODS

Ethical approval

As no live animals were used in this study, ethical approval from the institutional ethics review committee was not required.

Study area

The study was conducted in Hurulu Wewa reservoir (Figure 1), located in the North Central Province of Sri Lanka (8°11′–8°15′ N; 80°45′–80°48′ E). The reservoir primarily serves irrigation demands while simultaneously supporting an active inland fishery. According to the Department of Irrigation, the total catchment area delineated using GIS is 309,495 acres (125,248.2 ha), indicating a large upstream drainage basin contributing runoff during monsoonal rainfall events. The designated irrigable command area is 12,189 acres (4,932.7 ha), reflecting the reservoir's primary function as a water source for agricultural production. At Full Supply Level (FSL), the water-spread area extends to approximately 3,200 acres (≈1,295 ha), representing the maximum surface extent under full storage conditions.

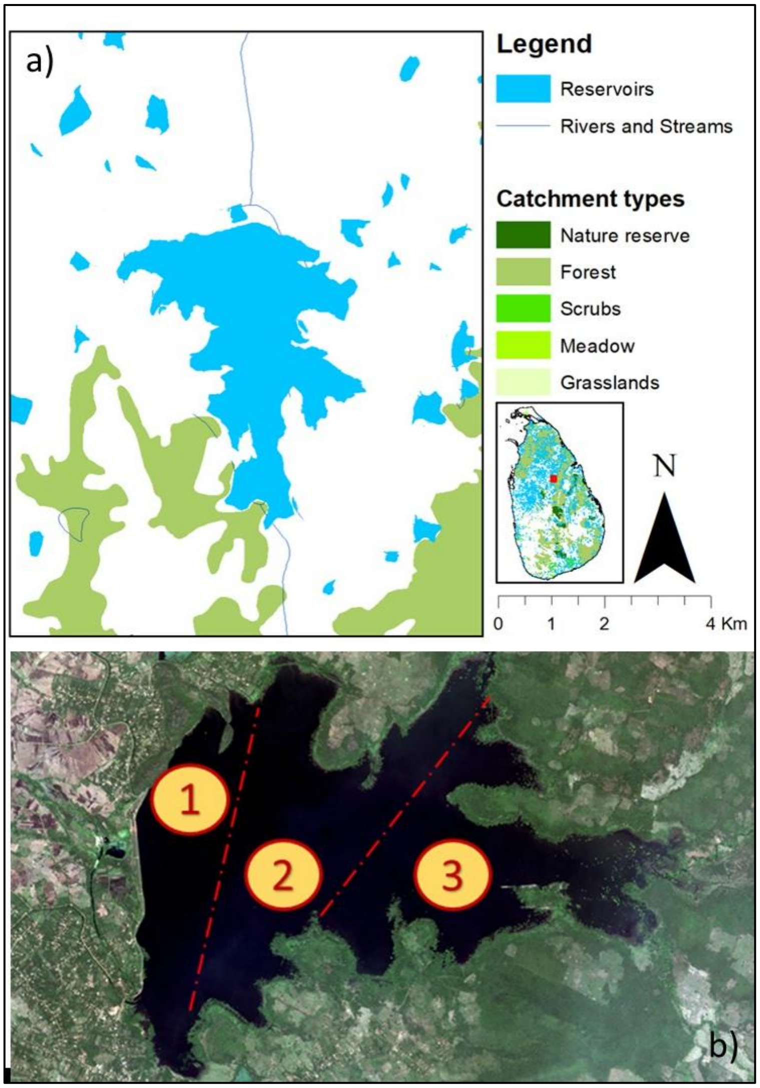

Fig 1. Study site and reservoir strata: (a) Hurulu Wewa reservoir (8°11′–8°15′ N; 80°45′–80°48′ E) and (b) identified three strata (1) Near downstream zone or reservoir embankment and spill (lacustrine and deepest area), (2) Transitional zone (moderately deep) and (3) Near upstream or lotic zone (shallow and mostly undulated area).

Hydrologically, the reservoir has a storage capacity at FSL of 67,800 acre-feet (83.6 million cubic metres), of which 52,966 acre-feet (65.3 million cubic metres) constitute live storage available for irrigation releases and regulated discharge. An additional 2,000 acre-feet (2.5 million cubic metres) is categorised as dead storage, which remains below the outlet sill level and is generally not utilisable for gravity irrigation. The Full Supply Level (FSL) is recorded at 132 m above Mean Sea Level (MSL), while the High Flood Level (HFL) is also documented at 132 m MSL, indicating the designed maximum operational water level. The Bund Top Level (BTL) is 135 m MSL, providing structural freeboard for flood safety.

Data collection

Monthly fisheries monitoring was conducted from June 2020 to April 2021, encompassing both dry and wet seasonal phases. Catch data of the GFP, were obtained through a systematic review of fishermen's logbooks and purchase records of collectors operating at the reservoir. Data extracted included total male catch (kg) and total female catch (kg) per month. Average individual body weight for each sex was estimated based on enumerated records maintained by fish collectors, who routinely documented size grades during purchase transactions. Using sex-specific mean weights, numerical abundance was derived as:

nM = (Total male catch in kg × 1000) / mean male weight (g) Eq 1

nF = (Total female catch in kg × 1000) / mean female weight (g) Eq 2

The monthly sex ratio was calculated as nM/nF. Further, participating fishers were instructed to maintain catch records separately to record each fishing operation, allowing the collection of operation-level, operation-area and species-specific catch data of GFP. Where spatially distinguishable catch information was available, data were categorised according to reservoir strata (riverine, transitional and lacustrine; Thornton *et al.*, 1990) based on fishing ground identification provided by fishers during the research discussions and personal interviews.

Hydrological data

Hydrological variables were obtained from the Department of Irrigation, Sri Lanka. Daily records included rainfall (mm), reservoir outflow (acre-feet; acft), reservoir water depth (ft) and storage capacity (acft). Monthly summaries were derived for analytical consistency with fisheries data. Rainfall values represented cumulative monthly precipitation within the reservoir catchment. Outflow data reflected irrigation releases and spill discharges. Storage capacity and depth were used as integrative indicators of water availability and hydrodynamic state.

Statistical analysis

Descriptive statistics were computed to summarise temporal trends in total catch, estimated counts (nM, nF) and sex ratios (nM/nF). Monthly and spatial variations in prawn abundance across reservoir strata were visually and statistically examined. Differences in sex ratio among reservoir strata were assessed using the non-parametric Kruskal–Wallis test due to deviations from normality. Where significant differences were detected, Dunn's post-hoc multiple comparison test with Bonferroni adjustment was applied to identify pairwise contrasts. Pearson or Spearman correlation analyses (depending on data distribution) were conducted to examine associations among hydrological variables (rainfall, outflow, depth and storage capacity). To explore non-linear hydrological interactions, Generalised Additive Models (GAMs) were fitted using the mgcv package in R. The following model structures were specified:

Depth ~ s(Capacity) Eq 3

Outflow ~ s(Capacity) Eq 4

Capacity ~ te(Rainfall, Outflow) Eq 6

Smooth functions (s) and tensor product smooths (te) were employed to capture potential non-linear and interactive effects. Model adequacy was evaluated using adjusted R^2, generalised cross-validation (GCV) scores and residual diagnostics. Here, all statistical analyses were performed using R statistical software (RCoreTeam, 2020), with significance evaluated at $\alpha = 0.05$.

RESULTS

Monthly monitoring of *Macrobrachium rosenbergii* populations was conducted from June 2020 to April 2021 across three ecologically distinct strata of the Hurulu Wewa reservoir. The sampling framework generated 24 strata–month combinations for sex-ratio analysis, supported by 304 daily hydrological observations aggregated into monthly summaries. The reservoir exhibited pronounced longitudinal zonation consisting of a deep lacustrine zone near the embankment (Stratum 1), a moderately deep transitional mid-basin (Stratum 2) and a shallow upstream lotic-influenced zone (Stratum 3). This stratified spatial design enabled examination of both structural habitat partitioning and hydrologically mediated redistribution processes within a lentic culture-based fishery system. In Sri Lankan inland reservoir fisheries, fishing is mainly carried out using gillnets from non-mechanised traditional boats, reflecting the artisanal nature of the sector. These nets are typically nylon with mesh sizes between 5–8 cm, providing size-selective harvest of dominant species while avoiding smaller fish, since monofilament nets are banned.

Overview of catch and count structure

Across the entire reservoir, males numerically dominated the population throughout the study period. Mean monthly male catch reached 660.29 ± 120.28 kg, substantially exceeding female catch, which averaged 127.03 ± 32.69 kg (Table S1). Similarly, mean male counts (2,530.17 ± 477.94 individuals) were approximately four times greater than female counts (615.10 ± 145.17 individuals). Total monthly counts averaged 3,145.27 ± 550.77 individuals, indicating strong overall productivity but pronounced sex asymmetry.

Average biomass per individual showed limited variation between strata and sexes, with mean male biomass of 0.23 ±0.02 kg and female biomass of 0.17 kg ± 0.02 (Table S1). The relative consistency in biomass across strata suggests that spatial differences in realised catch were primarily driven by differences in numerical abundance rather than major shifts in size structure (Figure 2). Therefore, spatial heterogeneity in catch weight largely reflected aggregation intensity rather than growth disparities.

Spatial variation across strata

When disaggregated spatially, marked heterogeneity became evident. Stratum 2 consistently exhibited the highest male abundance (Figure 2), with a mean monthly male catch of 1,153.62 ± 270.15 kg and mean counts of 4,421.33 ± 1,078.97 individuals (Table 1). Stratum 3 displayed intermediate male abundance (594.93 ± 127.64 kg; 2,269.46 ± 539.21 individuals), whereas Stratum 1 showed substantially lower male representation (232.31 ± 52.12 kg; 899.73 ± 230.06 individuals). This pattern indicates a strong gradient of male aggregation increasing from the lacustrine zone toward the transitional and upstream zones.

Table 1 Summary of Giant freshwater catch and counts across months and strata. Here, SD: Standard deviance; SE: Standard error; Min: Minimum and Max: Maximum.

Strata	Measures	Mean (per Month)	SD	SE	Min	Max
Stratum 1	Male Catch (Kg)	232.31	164.83	52.12	0.00	429.10
Stratum 2	Male Catch (Kg)	1153.62	854.30	270.15	0.00	2256.80
Stratum 3	Male Catch (Kg)	594.93	403.65	127.64	0.00	1015.30
Stratum 1	Average Biomass of Male (Kg)	0.23	0.14	0.04	0.00	0.40
Stratum 2	Average Biomass of Male (Kg)	0.23	0.14	0.04	0.00	0.40
Stratum 3	Average Biomass of Male (Kg)	0.23	0.14	0.04	0.00	0.40
Stratum 1	Counts of Male (nM)	899.73	727.51	230.06	0.00	2121.50
Stratum 2	Counts of Male (nM)	4421.33	3411.99	1078.97	0.00	8167.50
Stratum 3	Counts of Male (nM)	2269.46	1705.12	539.21	0.00	4984.00
Stratum 1	Female Catch (Kg)	174.10	237.88	75.23	0.00	722.10
Stratum 2	Female Catch (Kg)	151.94	190.85	60.35	0.00	652.00
Stratum 3	Female Catch (Kg)	55.04	36.90	11.67	0.00	106.90
Stratum 1	Average Biomass of Female (Kg)	0.17	0.10	0.03	0.00	0.30
Stratum 2	Average Biomass of Female (Kg)	0.17	0.10	0.03	0.00	0.30
Stratum 3	Average Biomass of Female (Kg)	0.17	0.10	0.03	0.00	0.30
Stratum 1	Counts of Female (nM)	766.25	929.19	293.84	0.00	2888.40
Stratum 2	Counts of Female (nM)	798.03	974.91	308.29	0.00	3260.00
Stratum 3	Counts of Female (nM)	281.01	191.85	60.67	0.00	600.00
Stratum 1	Total counts (nT)	1665.99	1179.14	372.88	0.00	3417.26
Stratum 2	Total counts (nT)	5219.36	4099.83	1296.48	0.00	10782.67
Stratum 3	Total counts (nT)	2550.47	1876.25	593.32	0.00	5584.00

Female distribution contrasted with male dominance patterns. Female counts were relatively similar between Stratum 1 (766.25 ± 293.84 individuals) and Stratum 2 (798.03 ± 308.29 individuals), while Stratum 3 exhibited markedly lower female abundance (281.01 ± 60.67 individuals). Female catch weights followed a comparable distribution, with Stratum 1 and Stratum 2 supporting higher female catches relative to Stratum 3 (Figure 2). These findings indicate partial spatial segregation between sexes, with females comparatively more represented in deeper lacustrine and transitional habitats and less prevalent in shallow upstream areas.

Stratum 1 displayed lower overall male dominance and occasionally approached near parity between sexes during certain months. In contrast, Stratum 2 and Stratum 3 exhibited sustained male dominance throughout the monitoring period (Figure 2). The persistence of this pattern across months suggests structural spatial partitioning rather than stochastic redistribution.

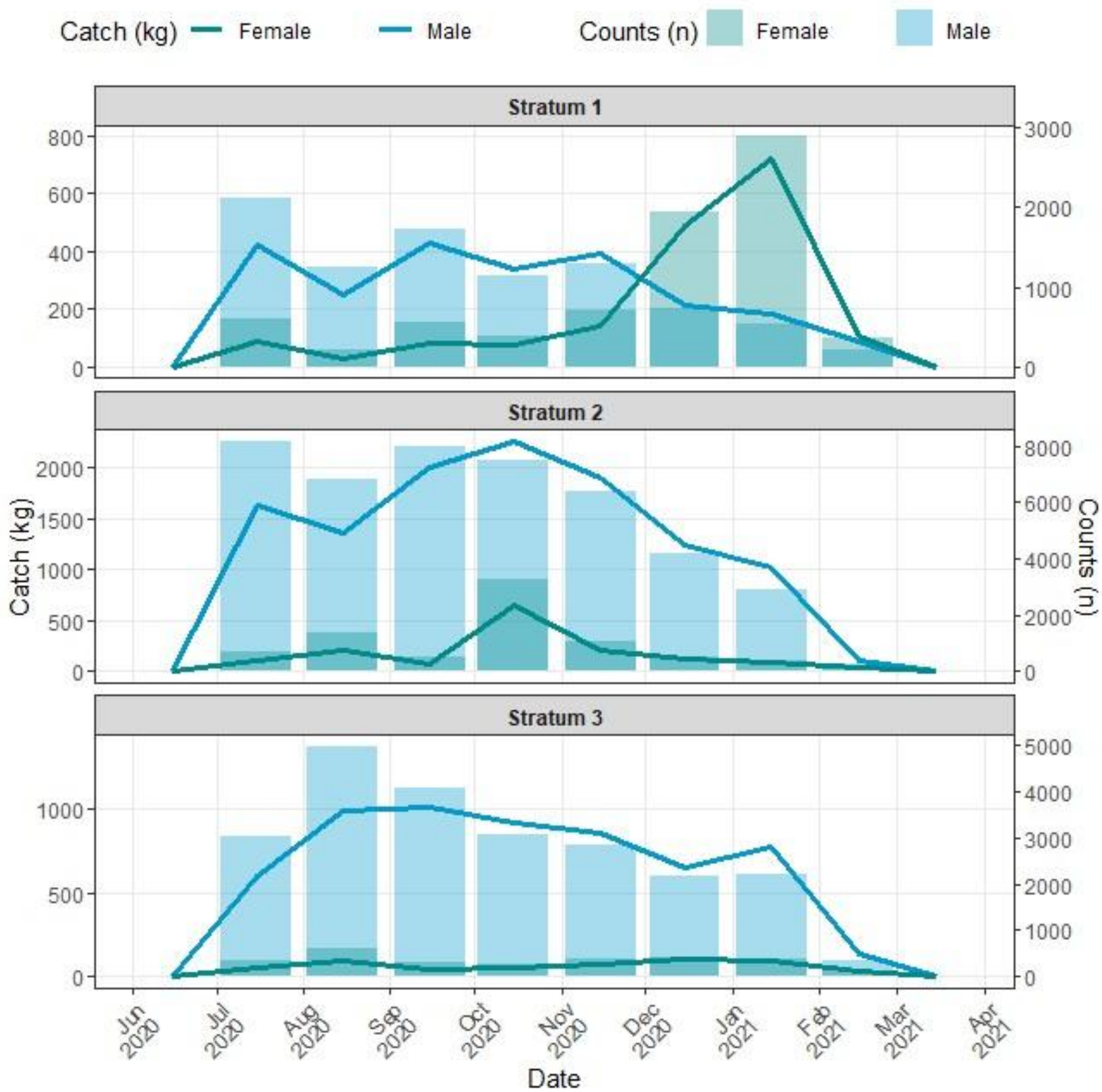

Fig 2. Catch and count variations of both Male and Female Giant freshwater prawns along the months and across the studied strata (top-bottom). Here, the line plots implicate the realised catches and bar plots shows the counts.

Sex ratio dynamics

Sex ratio (nM/nF) analysis provided quantitative confirmation of spatial segregation. Median sex ratios were 2.39 in Stratum 1, 6.77 in Stratum 2, and 7.91 in Stratum 3 (Table 2). The increasing gradient from Stratum 1 to Stratum 3 indicates intensified male aggregation toward upstream habitats.

The Kruskal–Wallis rank sum test demonstrated statistically significant differences in sex ratio among strata (p = 0.01), confirming that spatial variation in sex structure was unlikely to be due to random variation. Post hoc Dunn's multiple comparison tests with Bonferroni adjustment revealed a significant difference between Stratum 1 and Stratum 3 (p = 0.01), a marginal difference between Stratum 1 and Stratum 2 (p = 0.07), and no significant difference between Stratum 2 and Stratum 3. These results identify the principal spatial contrast as occurring between the lacustrine zone and the upstream lotic zone, while the transitional and upstream zones exhibit comparable levels of male aggregation.

Table 2 Summary of medians of Giant freshwater prawn sex rations across stratums and along months

Strata	**Median**	**Q1**	**Q3**	**IQR**
Stratum 1	2.39	0.543	3.15	2.61
Stratum 2	6.77	4.27	9.1	4.83
Stratum 3	7.91	5.77	9.65	3.88
Kruskal-Wallis rank sum test				
	df	**chi-squared**	**p-value**	**sign.**
	2	8.96	0.01133	**
Dunn multiple comparison p-values adjusted with the Bonferroni method.				
Comparison	**df**	**Z**	**p-adj**	**sign.**
Stratum 1-2	7	-2.2627	0.07095	*
Stratum 1-3	7	-2.8284	0.01403	**
Stratum 2-3	7	-0.5657	1	ns

* Significant at 0.10 probability level; ** Significant at 0.02 probability level; ns – Not significant.

Importantly, month-wise Kruskal–Wallis tests within each stratum did not detect significant temporal variation in sex ratio. This absence of significant within-stratum monthly fluctuation indicates that spatial structuring remained persistent throughout the study period (Figure 3). Thus, sex-specific habitat association appears to be driven primarily by structural habitat characteristics rather than short-term seasonal redistribution.

Temporal catch trends and hydrological context

Realised catch trends generally paralleled count patterns, with male catch weight consistently highest in Stratum 2 and Stratum 3. However, peak rainfall months did not directly correspond to peak catch values (Figure 4a and Figure 2). Rainfall exhibited episodic pulses associated with monsoonal events, with monthly maxima reaching 327.2 mm (Table S2). Despite these pulses, rainfall showed weak direct correlation with prawn counts.

Outflow exhibited distinct discharge phases, including periods of complete cessation and periods of substantial release, with monthly maxima exceeding 550 acft (Table S2). Three hydrological phases were identifiable: inflow-dominated phases characterised by rainfall without substantial discharge; transition phases marked by simultaneous inflow and outflow; and outflow-dominated phases during which discharge exceeded inflow contribution (Figure 4b).

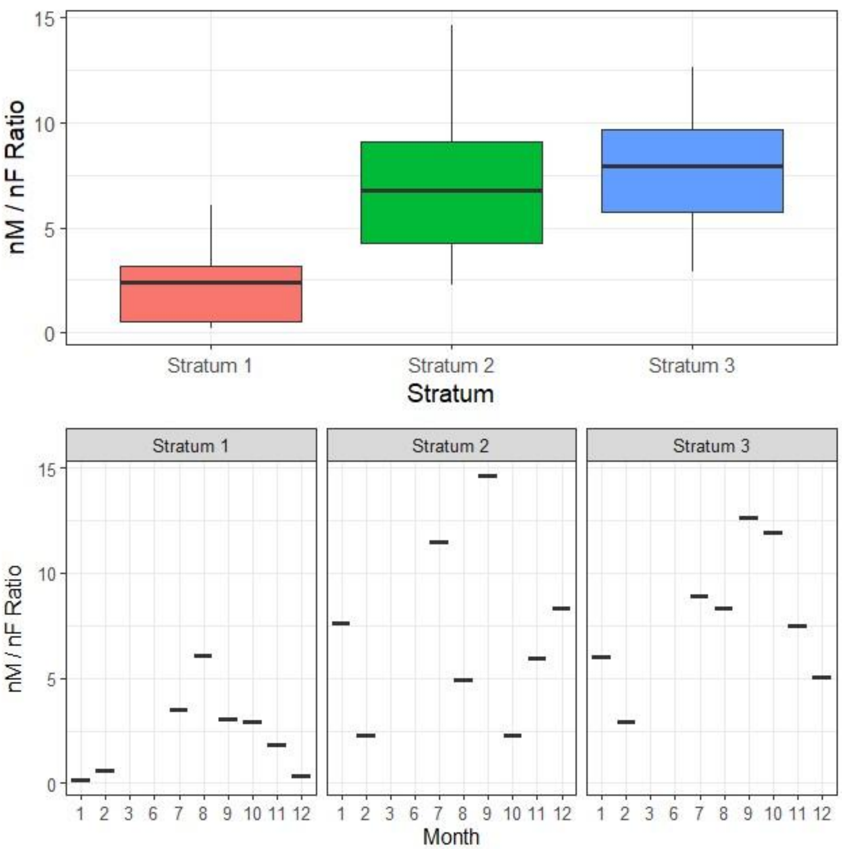

Fig 3. Sex ration (Male /Female count) (nM/nF) variations 0f Giant freshwater prawns in Hurulu Wewa across the strata and along the months In the x axis 1 stands for the June 2020 and respectively increase up to April 2021.

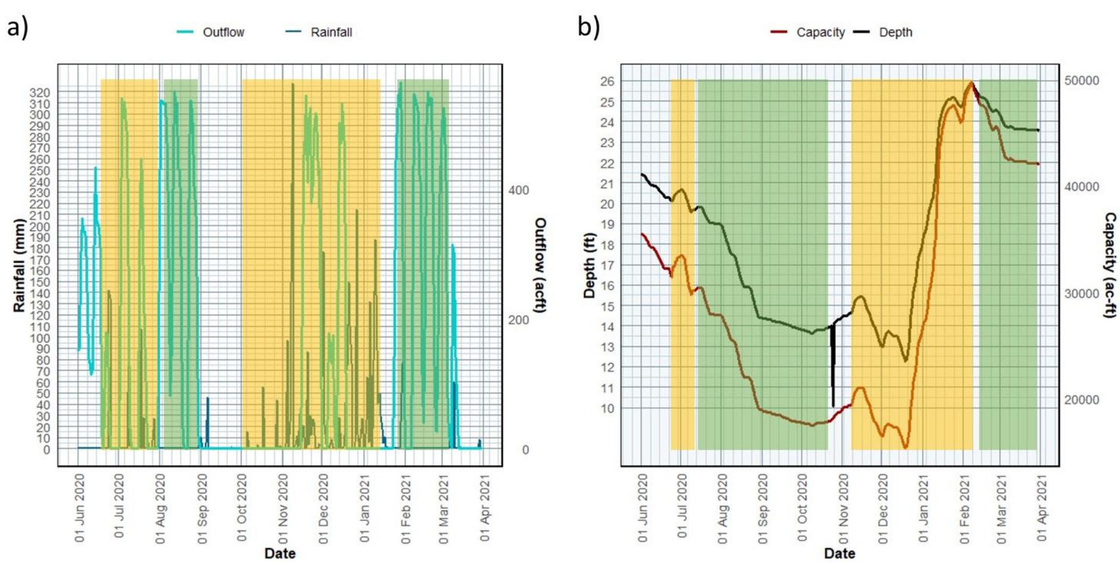

Fig 4. Temporal dynamics of (a) rainfall (mm) (blue) and reservoir outflow (acft) (cyan), and (b) reservoir depth (mm) (black) and storage capacity (acft) (red) in Hurulu Wewa from June 2020 to April 2021. Shaded areas highlight periods of concurrent inflow and outflow (yellow) and outflow-dominated periods (green).

Catch intensification, particularly of males in Stratum 3, appeared more closely associated with transitional hydrological phases than with rainfall magnitude alone. This suggests that hydrological state and flow gradients may influence prawn availability and spatial aggregation more strongly than precipitation intensity *per se*.

Hydrological regime characteristics

Hydrological analysis demonstrated substantial variation in reservoir depth and storage capacity over the monitoring period (Figure 5). Mean depth was 18.47 ft (5.6 m), with values ranging from 10.05 ft (3.1 m) to 25.9 ft (7.9 m) (Table S2 and S3). Capacity averaged 28,993.65 acft (35.8 million cubic metres) and reached a maximum of 49,700 acft (61.3 million cubic metres). Depth and capacity increased markedly during early 2021, reflecting substantial storage accumulation following monsoonal rainfall (Table S3).

Generalised Additive Models (GAMs) provided insight into structural relationships among hydrological variables. The model examining Depth as a smooth function of Capacity showed an almost perfect fit (p = 0.000) (Table 3), confirming strong bathymetric control. As capacity increased, depth responded in a smooth non-linear manner consistent with reservoir morphology (Figure 6). This near-perfect structural coupling indicates that habitat availability across strata is fundamentally governed by storage dynamics.

In contrast, the model evaluating Outflow as a function of Capacity explained only 7.88% of deviance (p = 0.0002) (Table 3), indicating that discharge is only partially determined by storage and is likely influenced by irrigation management decisions. The interaction model (Table 3), was statistically significant (p = 0.006) but explained only 6.68% of deviance, suggesting that short-term inflow–outflow interactions contribute modestly to capacity fluctuations (Figure 7), while longer-term storage patterns dominate.

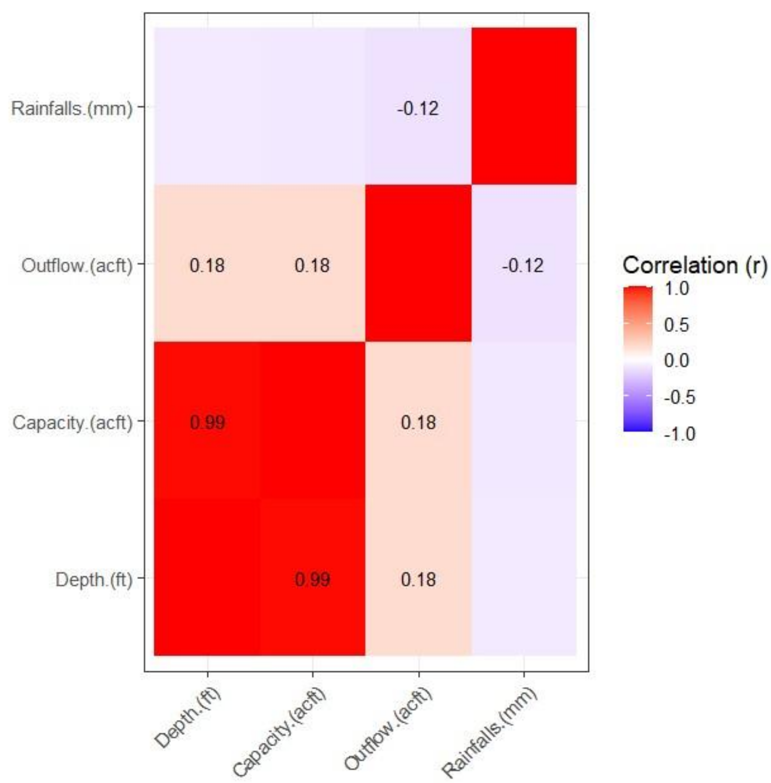

Fig 5. Correlation among the studied hydrological parameters

Table 3 Generalised additive model (GAM) summary and level of significance

Models	edf	REML	p-value	R-sq adj	Explained Deviance (%)
Depth ~ s(Capacity)	3.894	17.327	0.0000	0.997	99.7
Outflow ~ s(Capacity)	3.411	2030.7	0.0002	7.88	7.88
Capacity ~ te(Rainfall, Outflow)	5.078	3214.8	0.00598	0.0499	6.68

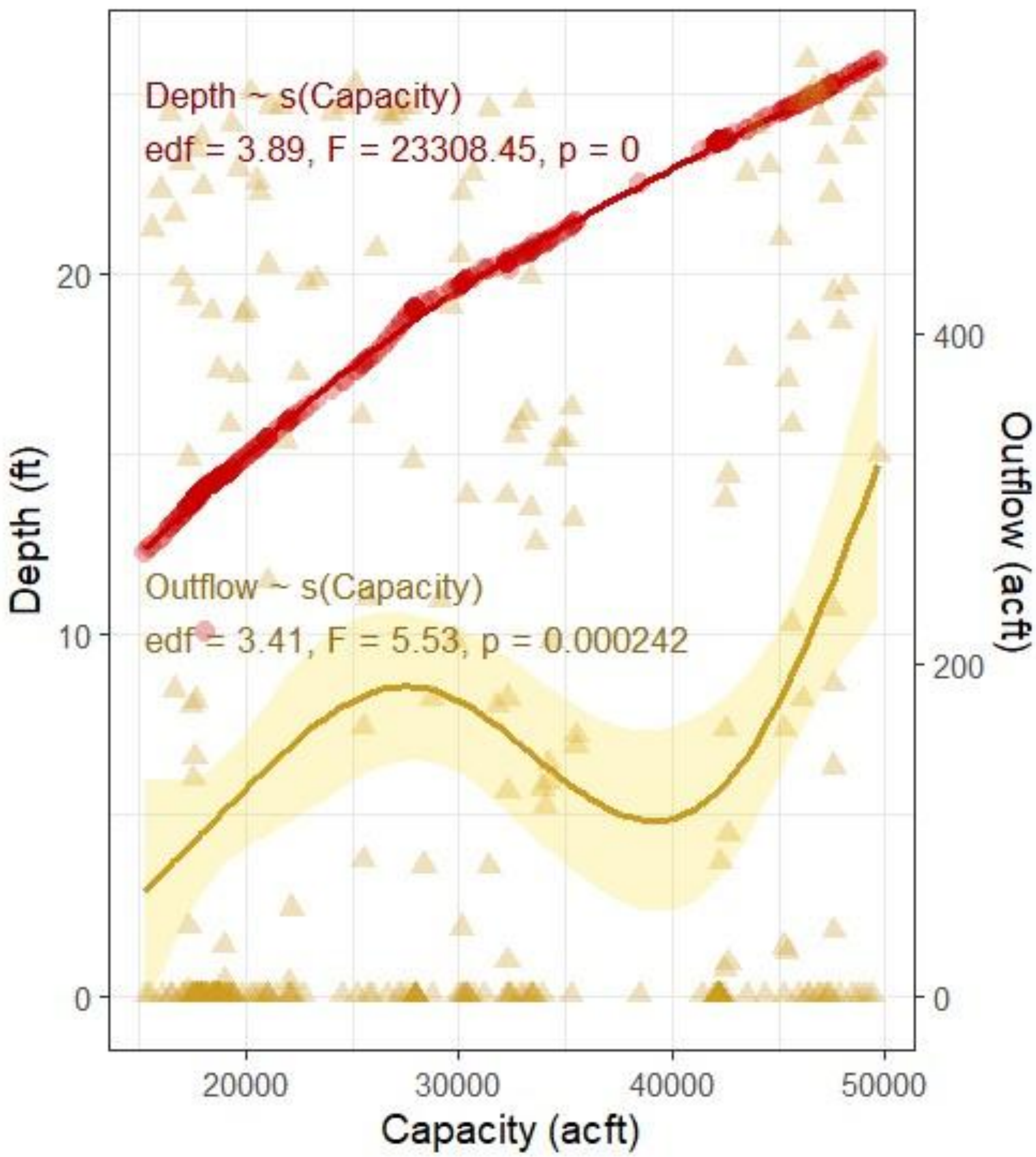

Fig 6. Generalized additive model (GAM) plot showing the smooth relationship between reservoir storage capacity and (a) water depth, and (b) outflow of Hurulu Wewa

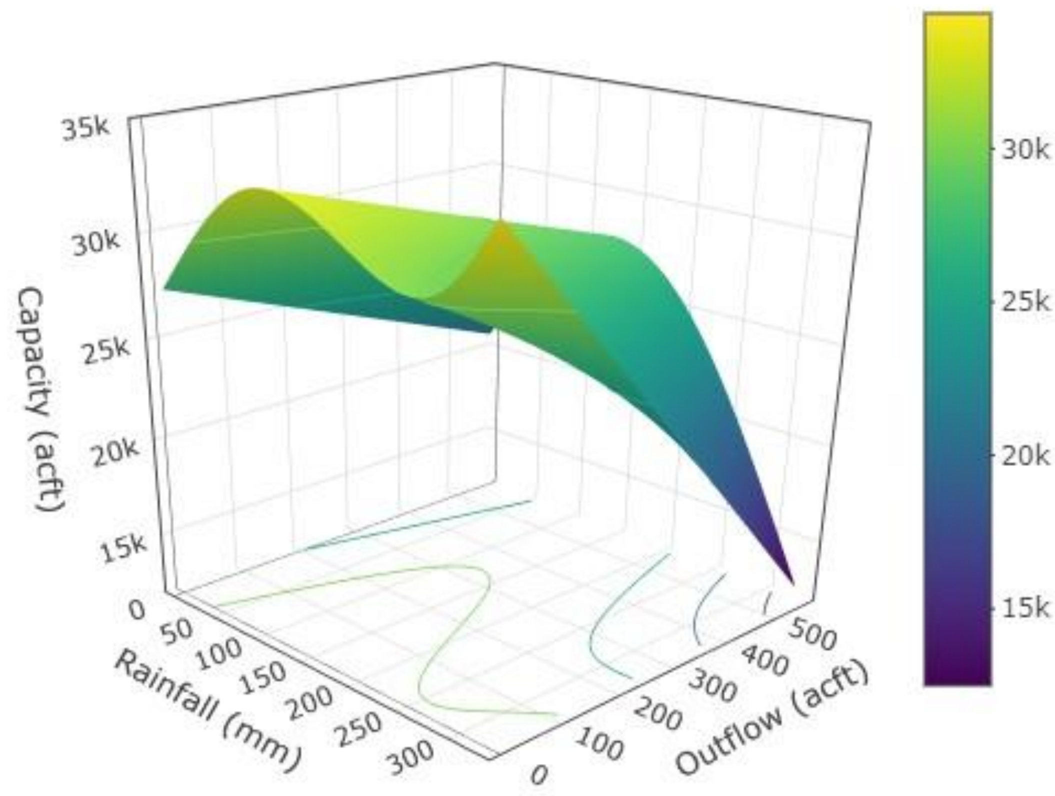

Fig 7. Three-dimensional model of some hydrological parameters of Hurulu Wewa collected during 2020-2021

Correlation analysis in Figure 8, further demonstrated a strong positive association between depth and capacity, weak direct correlation between rainfall and prawn counts, and modest association between outflow and upstream male counts. These findings reinforce the conclusion that structural hydrological configuration, rather than rainfall magnitude alone, shapes biological responses.

Hydrology–biology coupling across strata

Periods characterised by simultaneous inflow and outflow corresponded with observable increases in male dominance in Stratum 3 (Figure 9). This pattern suggests that moderate flow gradients may stimulate upstream orientation or territorial aggregation in shallow, undulating substrates. The upstream zone likely provides favourable habitat conditions during moderate depth states when shallow margins expand and habitat complexity increases.

Stratum 1 maintained comparatively stable sex ratios throughout hydrological pulses (Figure 9), indicating reduced responsiveness to short-term flow changes. The deeper lacustrine zone likely buffers rapid hydrological fluctuations, providing more stable environmental conditions. The relatively higher female representation in this zone suggests a potential refuge function or preference for deeper, less hydrodynamically variable habitats.

Stratum 2 exhibited persistent high male dominance similar to Stratum 3 but with less pronounced fluctuation during hydrological transitions (Figure 9). This intermediate behaviour suggests that the transitional zone may function as an ecological interface or redistribution corridor linking deep lacustrine and shallow upstream habitats.

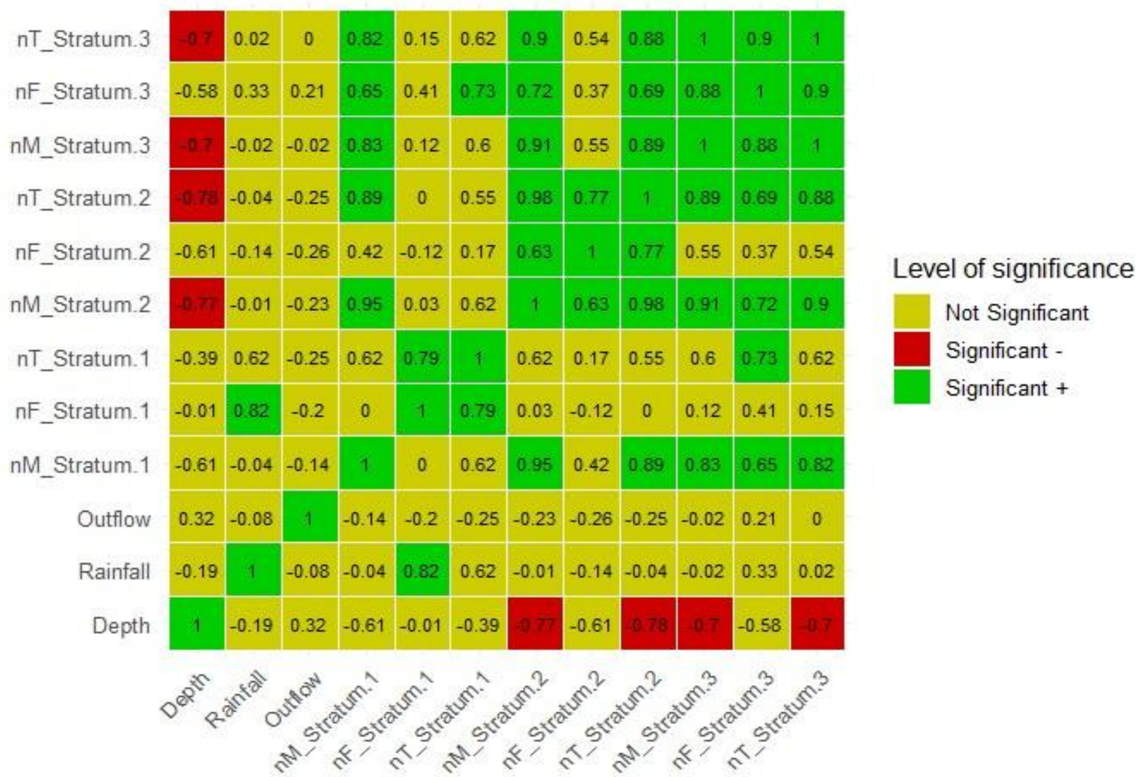

Fig 8. Correlation among the studied hydrological parameters and giant freshwater prawn counts across strata

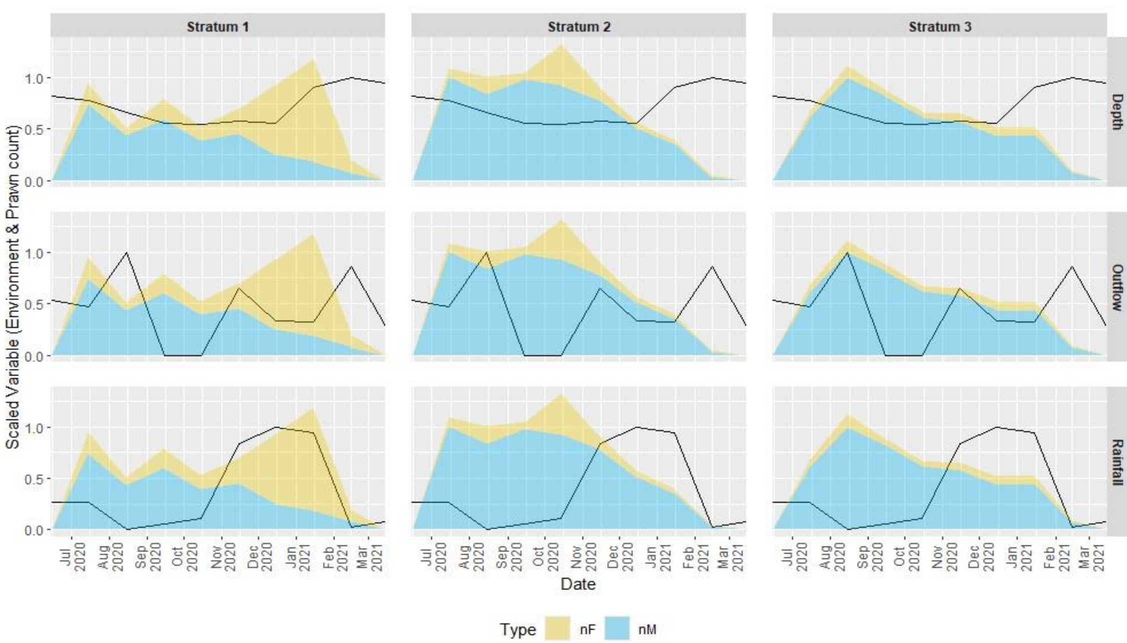

Fig 9. Monthly dynamics of (a) male and (b) female *M. rosenbergii* counts across the three reservoir strata in relation to (c) rainfall and (d) outflow. The vertical grey bar highlights a period of transitional hydrology (concurrent inflow and outflow) associated with increased male abundance in the upstream stratum (Stratum 3)

Integrated interpretation of directional dynamics

Three converging lines of evidence support the presence of intra-reservoir directional tendencies. First, statistically significant stratum-wise differences in sex ratio confirm persistent spatial segregation. Second, the absence of significant month-wise variation within strata indicates that this segregation is structurally stable rather than seasonally transient. Third, the association between hydrological transition phases and intensified male dominance in the upstream zone suggests flow-mediated redistribution. Although direct tagging or movement data were not available, the coupling between transitional hydrology and upstream male aggregation provides indirect evidence of directional movement influenced by flow gradients. The data do not support random dispersal (Table S4); instead, they indicate structured aggregation patterns linked to reservoir zonation and hydrological state.

Collectively, these findings demonstrate that spatial heterogeneity dominates over temporal variability within the Hurulu Wewa reservoir. Hydrological storage dynamics define habitat configuration, while externally regulated discharge pulses introduce short-term gradients capable of modulating aggregation intensity. The lacustrine zone exhibits comparatively lower male dominance and greater stability, whereas transitional and upstream zones consistently support elevated male aggregation. Overall, the results provide strong quantitative evidence for persistent intra-reservoir zonation of *M. rosenbergii* and suggest hydrologically influenced directional tendencies within this lentic CBF system.

DISCUSSION

The present investigation demonstrates that the population structure of GFP in Hurulu Wewa reservoir is primarily shaped by spatial configuration rather than by short-term temporal fluctuation. The persistence of significant sex-ratio differentiation among ecological strata, alongside the absence of statistically meaningful month-wise variation within those strata, confirms that the distributional pattern is structurally maintained. In practical terms, this indicates that the reservoir does not function as a homogeneous production basin, as is often implicitly assumed in CBF as in other aquaculture systems, but rather as a spatially compartmentalised system in which ecological gradients consistently regulate biological organisation.

The comparatively lower male dominance in the lacustrine stratum relative to transitional and upstream zones suggests that depth and hydrodynamic stability act as primary organising forces. However, it must not be ruled out that the differences in catchability of male and female GFP may also influence the occurrence of both sexes in the landings, which was not addressed in the present analysis. The deep lacustrine area provides a buffered environment characterised by reduced flow variability and enhanced physical stability. Such conditions may promote female association, possibly reflecting energetic efficiency, reproductive security or predator avoidance strategies (Malecha, 2012). In contrast, the upstream and transitional strata are shallower, structurally heterogeneous and periodically influenced by flow cues (Juarez *et al.*, 1987). These features are consistent with ecological settings that favour male territorial aggregation and hierarchical dominance, traits widely documented in *M. rosenbergii*.

An important consideration in interpreting these spatial patterns is the potential for sex-specific or habitat-specific catchability to influence the observed sex ratios. If males were simply more vulnerable to fishing gear in shallow, structured habitats, or females were highly catchable in deeper zones, the observed sex ratio gradients could reflect sampling bias rather than true biological segregation. Several lines of evidence suggest this is unlikely to fully explain our results. First, the average individual biomass of both males and females remained remarkably consistent across all three strata throughout the study period (Table 1). If catchability varied substantially by habitat, we might expect to see systematic differences in the size composition of catches, for example, only larger, more vulnerable males being caught in shallow zones, which was not observed. Second, the spatial patterns persisted across multiple months despite varying hydrological conditions (Figure 3), indicating structural stability inconsistent with stochastic gear-related biases. Third, the logical temporal coupling between hydrological transition phases and intensified upstream male aggregation (Figure 9) points toward a biologically meaningful behavioural response rather than a static artefact of fishing efficiency. Nevertheless, without direct underwater observation or telemetry data, we cannot completely rule out some contribution of catchability differences. However, the convergence of multiple lines of evidence, consistent size structure, temporal stability and hydrologically linked variation, strongly supports the interpretation that the observed spatial structuring reflects genuine ecological preferences and flow-mediated redistribution of *M. rosenbergii* in this reservoir system.

Moreover, while our data strongly suggest flow-mediated directional redistribution, future studies employing telemetry or mark-recapture techniques are needed to confirm individual-level migration trajectories.

The recurrent male dominance observed in the transitional and upstream zones aligns with the species' behavioural ecology, in which larger males compete for structurally advantageous territories. Although morphotype differentiation was not quantified, the elevated male ratios imply preferential occupation of habitats that optimise feeding opportunities and competitive positioning. The transitional zone, situated between deep lentic and shallow lotic conditions, appears to provide a functional compromise between environmental stability and resource accessibility. The upstream zone, characterised by variable substrate exposure and occasional directional flow, likely enhances benthic productivity and reinforces competitive territoriality.

Although Hurulu Wewa reservoir lacks an extensive lateral floodplain, its longitudinal gradient—from deep lacustrine waters to shallow upstream margins—functions as a scaled analogue of riverine spatial structuring. Rather than seasonal expansion across floodplains, habitat heterogeneity is organised along depth and hydrodynamic axes. The persistence of sex-specific zonation therefore reflects ecological compartmentalisation similar in principle to that observed in large flood-pulse systems (Martin *et al.*, 2013; Maitland *et al.*, 2024).

Hydrological conditions in the reservoir appear to function as behavioural modifiers rather than direct abundance determinants. Rainfall magnitude alone showed limited explanatory power with respect to prawn redistribution. Instead, transitional phases characterised by concurrent inflow and irrigation-driven outflow were associated with intensified upstream male aggregation. This distinction between precipitation and actual flow gradient is ecologically significant. In regulated rivers such as the Nile River, altered discharge timing following dam construction disrupted migratory cues more profoundly than rainfall variability itself, resulting in modified catch structures and species composition (Welcomme, 2008). Similarly, reservoir studies in Thailand have demonstrated that abrupt discharge events shortly after stocking increase downstream drift and reduce effective yield (Jutagate, 2009; Jutagate *et al.*, 2012; Jutagate and Kwangkhang, 2015).

The amphidromous evolutionary background of *M. rosenbergii* provides a plausible mechanistic explanation for its sensitivity to transitional hydrological cues. Although landlocked reservoir populations no longer complete downstream larval development in estuarine environments, rheotactic orientation remains a conserved behavioural trait (New, 2000a, b; New *et al.*, 2000). Comparable flow-mediated migration persists in other amphidromous or catadromous taxa such as *Anguilla japonica*, where subtle hydrodynamic gradients stimulate upstream colonisation. Even in impounded systems, residual rheotactic sensitivity may promote longitudinal redistribution in response to artificial flow pulses.

Migration-mediated redistribution frequently influences fisheries through spatial concentration rather than net population change. In African floodplain rivers, fish aggregate during receding-water phases, temporarily elevating catch per unit effort (CPUE) while increasing exploitation pressure on reproductively active individuals (Welcomme *et al.*, 2014). Similar aggregation-driven catch variability has been documented in clupeid fisheries such as *Limnothrissa miodon*, where vertical and horizontal migrations alter gear efficiency and seasonal harvest intensity (Marshall, 1993). In South Asian reservoirs, upstream congregation of major carps including

Catla catla and *Labeo rohita* during hydrological stimulation has historically increased localised catch rates without necessarily reflecting overall biomass growth (De Silva and Funge-Smith, 2005; De Silva and Amarasinghe, 2009).

The intensified upstream male aggregation observed during transitional inflow and outflow phases in Hurulu Wewa reservoir aligns with these broader patterns. Redistribution along the longitudinal gradient likely enhances localised catchability while total stock abundance remains relatively stable. Consequently, CPUE variation may reflect behavioural concentration rather than recruitment or population expansion. Such dynamics are particularly relevant in CBF systems, where stocking success is often evaluated using short-term catch indicators.

Sex-specific habitat partitioning further complicates this dynamic. Male dominance in transitional and upstream strata suggests preferential occupation of structurally advantageous territories that optimise feeding opportunities and competitive positioning. Comparable sex-biased habitat use occurs in salmonids such as *Oncorhynchus mykiss*, where dominant males occupy energetically favourable territories during spawning migrations, displacing subordinate individuals (Pearse *et al.*, 2019). In decapod crustaceans, male territoriality frequently results in spatial clustering within optimal substrates (Juarez *et al.*, 1987). The asymmetrical responsiveness of males and females in the Hurulu Wewa reservoir implies that hydrological transitions disproportionately influence male redistribution, potentially altering harvest composition and long-term demographic balance if fishing effort is spatially concentrated.

The near-perfect coupling between depth and storage capacity emphasises bathymetry as the foundational structural determinant. Rising storage expands shallow littoral margins and inundates previously exposed substrates, increasing the availability of territorially favourable habitats. Conversely, declining storage compresses available habitat and intensifies spatial concentration. Despite these volumetric changes, proportional sex ratios among strata remained stable, indicating predictable behavioural responses to habitat configuration rather than stochastic dispersal during water-level fluctuation.

Anthropogenic hydrological regulation introduces an additional layer of ecological complexity. The relatively weak predictive relationship between outflow and storage capacity reflects irrigation management practices that partially decouple discharge from natural hydrological cycles (Nissanka *et al.*, 2000; Jutagate *et al.*, 2012). In Thai reservoirs, irrigation releases have been shown to transport stocked juveniles downstream, reducing retention efficiency and yield (Sripatrprasite and Lin, 2003). If transitional discharge phases simultaneously stimulate upstream orientation and create downstream transport pathways, escapement risk may increase. Thus, irrigation management decisions indirectly shape spatial behaviour, stock retention, and catch outcomes.

From the management perspective, recognising the Hurulu Wewa reservoir as a spatially structured and behaviourally responsive ecosystem has several operational implications. First, stocking strategies should be synchronised with periods of rising storage to maximise shallow habitat expansion and reduce density compression. Second, coordination between irrigation authorities and fisheries managers is essential to minimise escapement during discharge events, particularly immediately following stocking. Third, spatial harvest regulation may be necessary to prevent disproportionate removal of male-dominated aggregations in upstream and transitional zones. Designating lacustrine areas as partial refugia while regulating effort in aggregation zones could preserve demographic stability and social hierarchy.

At the policy level, the reservoir functions as a coupled hydrological–ecological system in which irrigation management decisions reshape habitat availability and behavioural distribution. Comparative evidence from floodplain fisheries and amphidromous prawn ecology collectively reinforces a central principle: migration, whether large-scale or intra-reservoir, profoundly influences catch dynamics through redistribution, aggregation and escapement processes. Effective CBF management must therefore integrate hydrological forecasting, ecological zoning, and adaptive harvest regulation rather than treating the reservoir as a uniform water body.

CONCLUSION AND REMARKS

This study provides clear quantitative evidence that the population structure of *M. rosenbergii* in Hurulu Wewa reservoir is governed primarily by persistent spatial gradients rather than short-term temporal variability. Significant sex-ratio differences among lacustrine, transitional and upstream strata, coupled with the absence of month-wise variation within strata, confirm stable intra-reservoir zonation. The lacustrine zone maintained comparatively lower male dominance, whereas transitional and upstream zones consistently exhibited elevated male aggregation. These findings indicate structural habitat partitioning along depth and hydrodynamic gradients. Hydrological conditions functioned as behavioural modifiers rather than direct abundance determinants: rainfall alone did not significantly predict prawn redistribution, but transitional phases characterised by concurrent inflow and outflow were associated with intensified upstream male aggregation. This pattern suggests that subtle flow gradients may activate rheotactic responses consistent with the species' amphidromous evolutionary background. The near-perfect coupling between storage capacity and depth further emphasises bathymetry as the fundamental structural determinant shaping habitat availability and spatial organisation. Future research employing telemetry or mark-recapture techniques is now needed to confirm individual-level migration trajectories and further elucidate the behavioural mechanisms underlying these patterns.

From the management perspective, recognising the reservoir as a spatially compartmentalised ecological system is critical. Accordingly, sustainable culture-based fisheries management in Sri Lankan reservoirs requires spatially explicit and hydrologically synchronised strategies. Integration of ecological zoning, irrigation–fisheries coordination, escapement mitigation and regulated harvesting of aggregation zones is essential to safeguard stocking investments and maintain long-term yield stability.

By situating Hurulu Wewa reservoir within the broader theoretical and empirical framework of inland migration ecology, this study advances understanding of how bathymetric structure, hydrological modulation, and behavioural adaptations interact to govern spatial organisation. Recognition of reservoirs as compartmentalized socio-ecological systems, rather than homogeneous production basins, is fundamental to achieving resilient and sustainable inland fisheries enhancement.

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DISCLOSURE STATEMENT

The authors declare that they have no competing interests.

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