Molecular characterization and pathogenicity assessment of bacteria causing infectious diseases in cage-farmed fish in the Lake Victoria

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SUMMARY

Cage aquaculture in Lake Victoria Tanzania has expanded rapidly increasing from 460 in 2021 to over 1000 in 2025, yet disease outbreaks remain a major constraint to productivity and farmer livelihoods. A cross-sectional study was conducted to investigate bacterial pathogens affecting Nile tilapia (*Oreochromis niloticus*) in cage farms across six districts in the Lake Victoria Basin (LVB), Tanzania. A total of 90 moribund fish were collected from thirty cage fish farm purposively and from each fish liver and kidney were sampled. Bacterial isolates were identified using biochemical profiling and 16S rRNA gene sequencing. Three pathogenic bacteria namely *Citrobacter freundii*, *Pseudomonas aeruginosa*, and *Streptococcus agalactiae* were isolated and identified. Pathogenicity trials demonstrated that *P. aeruginosa* exhibited the highest mortality rate (86.7%), followed by *C. freundii* (53.3%) and S. agalactiae (40%). Clinical and post-mortem findings from the trials showed symptoms consistent with haemorrhagic septicaemia, scale loss, fin rot, skin ulcer, Popeye, and eye loss. Phylogenetic analysis grouped sequences of each pathogen into a single cluster, regardless of their geographical origins, suggesting a common source and subsequent dispersal to various locations. The study calls for farmer training and harmonized efforts to strengthen disease control strategies, as farmers are likely dealing with the same bacterial strains.

Keywords: Cage Fish Farming, Pathogenic bacteria, Fish Diseases, Lake Victoria Basin (LVB).

Article History
Submitted: 11 Nov 2025
Revised: 22 Nov 2025
Accepted: 10 Dec 2025
Published: 10 Jan 2026

Tanzania Veterinary Journal Vol. 40(2) 2025
https://dx.doi.org/10.4314/tvj.v40i2.2
ISSN: 0856 - 1451 (Print)
ISSN: 2714-206X (Online)
https://tvj.sua.ac.tz

INTRODUCTION

Fish diseases pose a serious constrain to the expansion and development of sustainable aquaculture (Mukaila et al., 2023). In global aquaculture, the emergence of previously uncharacterized pathogens linked to novel and unknown diseases has become an emerging trend (Haenen et al., 2023). These pathogens typically spread rapidly, often transcending national boundaries, and cause major production losses approximately every 3–5years (El-Barbary & Hal, 2016; Haenen et al., 2023). The management efforts on the health of aquatic organisms have significantly increased during the last three decades (Haenen et al., 2023). However, such efforts have not kept pace with the rapid growth of the aquaculture sector (FAO, 2023). Many of the most serious infectious disease agents affecting cultured species in aquaculture are bacteria (Haenen et al., 2023). Bacteria rarely act as primary pathogens and are more commonly opportunistic pathogens in already immunocompromised hosts (Ndashe et al., 2023). Nevertheless, bacteria can cause significant losses in fish farming (Haenen et al., 2023).

Cage fish farming was introduced in Lake Victoria (LV) in 2005, and since then, the region has seen a rapid increase in the number of cages, with over 8,024 now installed in the LVB (Opiyo et al., 2018). This method has become more intensive, with stocking densities reaching up to 150 kg/m³, compared to traditional pond systems and other aquaculture methods in the region, which yield between 0.2 and 100 kg/m³ (Rutaisire et al., 2009). However, this expansion has been linked to significant losses from fish disease outbreaks, leading to

fish morbidity and mortality. Morbidity results into poor growth, reduced market price of the produce, and high costs for treatment and preventive measures (Rutaisire et al., 2009). According to the (World Bank & GAA, 2014), global revenue losses attributed to fish diseases were estimated at 6 billion USD in the past ten years. In developing countries, over 50% of fish production is lost due to diseases, with China, a leading aquaculture producer, reporting 15% loss of total fish production due to diseases (Leung et al., 2013; Ndashe et al., 2023).

In Tanzania, less attention has been given to fish diseases in cage-farmed fish. Often, bruises, abrasions, and hemorrhages are incorrectly attributed to only overstocking rather than microbial infections. As a result, the use of salt (NaCl) treatments has become a common practice (Emam et al., 2024). A few studies focusing on bacteria are limited to the identification of pathogens at the genus level (Walakira et al., 2014). This has left the status of fish bacterial pathogens and the associated diseases in cage fish farms poorly understood, increasing the likelihood that many fish diseases remain undiagnosed and continue to affect production. This knowledge gap leads to guesswork, with farmers often employing treatments that are incorrect or insufficient, thereby failing to address the actual causes of the diseases (Opiyo et al., 2018). The delayed detection of diseases further compounds the issue, hindering the implementation of effective control measures (Mwainge et al., 2021). This deficiency accelerates the occurrence and spread of fish diseases within the cage fish farms of the Lake Victoria Basin (LVB) (Akoll & Mwanja, 2012), leading to high mortality and discouraging farmers due to the increased economic loss. This study aimed to identify and characterise the different bacterial pathogens causing infectious diseases in cage-farmed fish in the Lake Victoria, Tanzania.

MATERIALS AND METHODS

Study area

The study was conducted in the LVB, Tanzania, involving the collection of diseased fish samples from six districts along the Tanzanian shoreline: Nyamagana, Sengerema, Busega, Rorya, Musoma Municipal Council (MC), and Musoma District Council (DC) (Fig. 1). These districts were purposively selected due to their high concentration of cage fish farming activities, collectively hosting over 1,000 active fish cages (URT, 2023). The rapid expansion and intensification of cage aquaculture in these districts have resulted in high stocking densities and close proximity of cages, increase the likelihood of disease occurrence and facilitate the spread of infectious pathogens within and between farms. The Lake Victoria shoreline in these districts is characterized by warm tropical conditions, with surface water temperatures ranging between 24–30°C, which favour pathogen survival and proliferation (Njiru et al., 2019). Additionally, biosecurity challenges such as limited routine disease screening, poor disposal of fish mortalities, inadequate cage spacing, and sharing of farm equipment without disinfection persist in the area, increasing the risk of disease transmission in cage-based aquaculture systems (Rhodes et al., 2023).

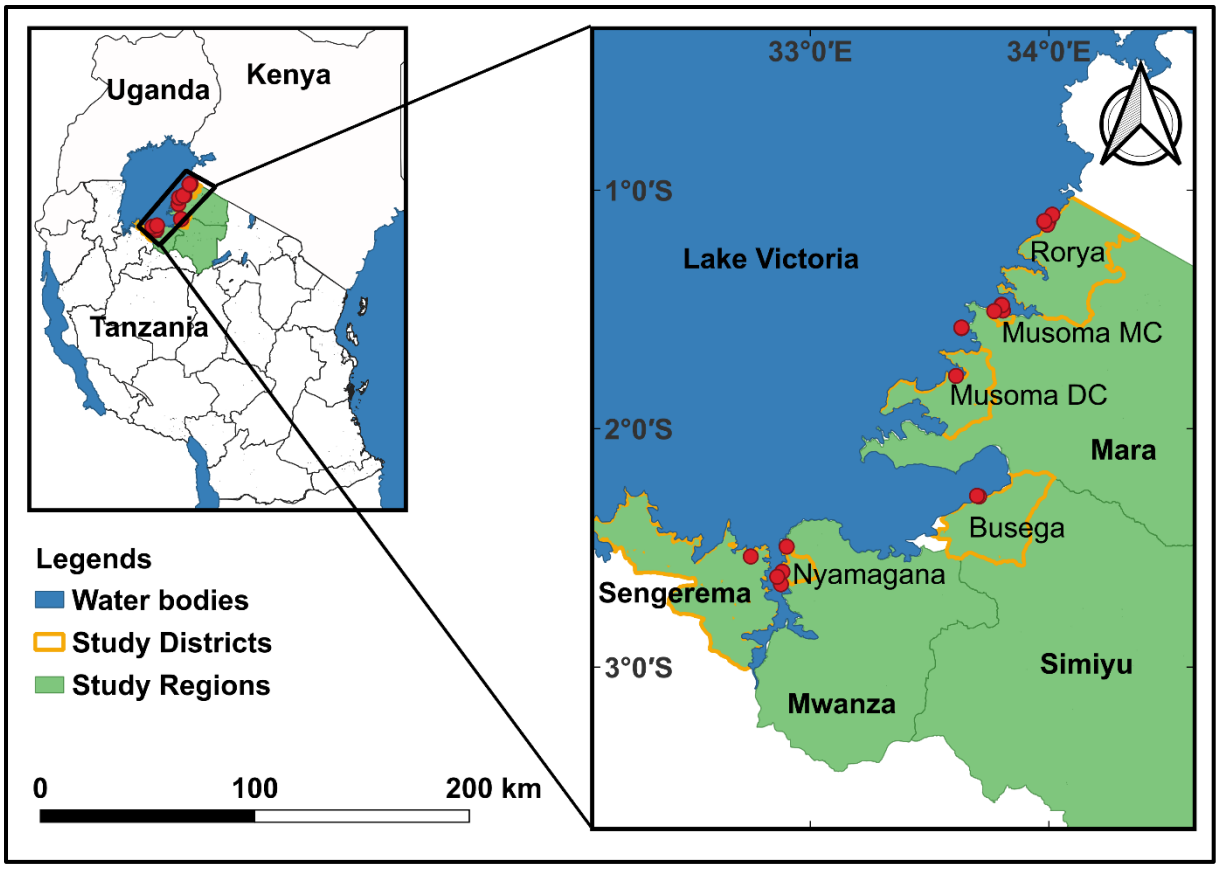

Figure1. Map of the study area showing locations where bacterial samples were collected from infected fish. The map was created using QGIS software version 3.28 and shapefiles from the Database of Global Administrative Areas (GADM) (https://gadm.org/maps/TZA.html, accessed on 27th February 2025).

Animal ethics

The handling of fish and all the experimental protocols were carried out according to the guidelines of the Animal Ethics, established by the Sokoine University of Agriculture Research and Ethical Committee permits number SUA/DPRTC/R/126/CONAS/15/2023/14. To alleviate suffering during sampling fish were initially treated with MS-222 (Tricaine Methanesulfonate).

Fish sampling in the LVB cage fish farming systems

A total of ninety Nile tilapia were sampled from cage farms between November and December 2024. Sampling was conducted in six study districts, with fifteen fish collected per district. In each district, three cage farms were selected, and five clinically diseased fish were sampled from each farm, giving a total of 30 cage farms. A purposive sampling strategy was employed, targeting fish exhibiting clinical signs of disease, including ulcerations, haemorrhages, exophthalmia, corneal opacity, eye loss, and scale loss according to (Algammal et al., 2020). Fish were carefully netted and handled to minimize stress, then humanely euthanized using tricaine methanesulfonate (MS-222) prior to sampling. Sterile swabs from liver, and kidney were placed in Stuart Transport Medium to preserve bacterial viability as applied by (Abdou et al., 2023). Samples were transported in insulated cooler boxes maintained at 4-8 °C and delivered to Sokoine University of Agriculture, Morogoro, within 72 hours, with temperature monitored throughout.

Isolation and identification of bacterial pathogens

Swabs collected from fish with clinical signs were directly placed onto Buffered peptone water and incubated at 37 °C for 24 hours for enrichment. Then, a loopful of incubated samples was taken and inoculated on Blood agar, *Pseudomonas* Lab agar, Mac Conkey agar, and Tryptic soy agar from Oxoid ltd media, UK and incubated at 37 °C for 24 hours, for isolation and identification of bacteria according to (Algammal et al., 2020). Presumptive colonies were selected based on distinct colony morphology, including size, shape, color, margin, elevation, hemolytic pattern on blood agar, pigmentation, and odor where applicable. All suspected colonies were purified by subculture for phenotypic and biochemical characteristics according to (Abdallah et al., 2024). All isolates were identified morphologically using Gram's stain and biochemically using various biochemical tests, including enzyme tests such as catalase test and series of profiles of sugars such as Sulphide, indole, and motility test (SIM test), and Triple sugar iron (TSI) (Abu-Elala et al., 2019). All laboratory procedures were conducted under biosafety level 2

(BSL-2) conditions, with appropriate use of personal protective equipment (laboratory coats, gloves, and masks) to ensure safety and prevent cross-contamination.

Molecular characterization of the isolated bacteria

The genomic DNA of the isolated Gram-negative bacteria was isolated using FlaPure Bacteria Genomic DNA Extraction Kit (Genesand Biotech Co., Ltd, Beijing, China) following the manufacturer's instructions. For the isolated Gram positive, the genomic DNA was isolated using the thermal extraction method in accordance to (Carriero et al., 2016). A 1.0 mL of the Tryptic broth culture was pelleted, washed, and resuspended by vortexing in nuclease free water (Sourced from Inqaba biotech, Hatfield, South Africa), placed in a water bath at 95 °C for 5 min and immediately transferred to the ice for 5 min. This procedure was repeated, and the suspension was centrifuged at 10,000 rpm for 10 min (Ripanda et al., 2023). The quality of DNA extracts was checked on a 1 % agarose gel (ABM, Richmond, Canada) prior to subsequent analysis.

This was followed by amplification of the fragments of 16S rRNA (about 1,450 base pairs) in a T100 thermocycler using the universal primers 27[F:5'-AGAGTTTGATCATGGCTCAG-3'] and 1492 [R: 5'-TACGGYTACCTTGTTACGACTT-3'] (Mzula et al., 2020). PCR was performed in a total volume of 35µL containing 12.7 µL H2O (RNase-free), 17.5µL master mix, 1.75µL BSA, and 1.05 µM of each primer and 1.0 µL DNA template according to (Ripanda et al., 2023). The amplification was done as follows; Initial denaturation steps at 95 °C for 3 min and followed by 35 cycles of denaturation at 95 °C for the 30 s, annealing at 58 °C for 30 s and extension at 72 °C for 1 min followed by terminal extension at 72 °C for 3 min (Mzula et al., 2021; Ripanda et al., 2023). The agarose gel (1.5%) stained with safe view (ABM, Richmond, Canada) was used to analyse PCR products by electrophoresis, the DNA ladder 100kb was used to confirm size of DNA (Figure 2). Subsequently, successful PCR amplifications were sequenced using Sanger's Dideoxy sequencing technology, (Microgen lab Amsterdam, Netherlands). The obtained 16S rRNA sequences were edited using BioEdit ver. 7.7.1. High-quality sequences were then aligned using MEGA ver.11 (Tamura et al., 2021). Using the Basic Local Alignment Search Tool (BLAST), each edited 16S rRNA sequence were compared to 16S rRNA barcode records published in the GenBank nucleotide database to confirm the taxonomic identity of each bacterium and the sequences that showed identity above 98.7% were used in subsequent analysis. Confirmed sequences were submitted to the National Center for Biotechnological Information (NCBI) under accession numbers PX171334-PX171387 and PX735952-PX735963 sequences were then collapsed using Ver 1.61. Additionally, three reference sequences of *S. agalactiae* isolated from Nile tilapia in China (accession numbers KF111293.1), *C. freundii* isolated from Nile tilapia in Japan (accession numbers AB548828) and *P. aeruginosa* isolated from Nile tilapia in China (accession numbers FJ194518.1) were retrieved from the GenBank Nucleotide database and aligned with sequences generated by this study to produce a multiple alignment of 607 base pairs.

Subsequently, the phylogenetic tree was constructed using BEAST ver 2.5 (Bouckaert et al., 2019), to assess the evolutionary relationships among bacteria species. The analysis employed a relaxed uncorrelated log-normal molecular clock and a general time- reversible evolutionary model, running for 10 million generations. The phylogenetic tree was annotated using TreeAnnotator ver 1.10 (Helfrich et al., 2019) and visualized using FigTree ver 1.4 (Sauvage et al., 2018).

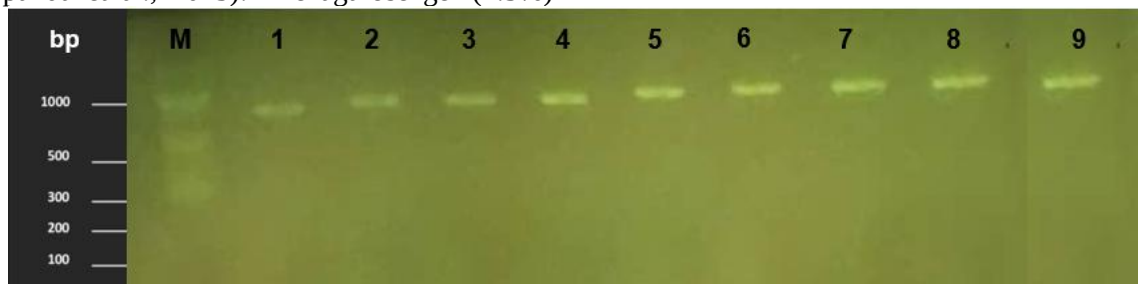

Figure 2. The agarose gel (1.5%) stained with safe view containing plasmid DNA of the indicated strains. Lane M is DNA size marker (100 bp DNA ladder). Lane 1, A positive control of *P. aeruginosa*; lanes 2-3 *P. aeruginosa* strains; lane 4, A positive control of *S. agalactiae* strains; lanes 5-6 *S. agalactiae* strains; lane 7, A positive control of *C. freundii* strains; lanes 8-9 C. freundii strains.

Pathogenicity test

Acclimation period

A total of 200 healthy Nile tilapia weighing 200 g with no history of previous infections were collected randomly from Blue Economy Research Center, Sokoine University of Agriculture, Tanzania, and left acclimated in a clean round concrete tank of $3m^3$ holding capacity for seven days prior to pathogenicity experiments. Tanks were filled with underground well water with an average salinity of 0.02 ± 0.003 g/L,

dissolved oxygen was monitored at 6±1 mg/L, while the water temperature was maintained at 27±0.52 °C. The fish were fed two times daily (09:00 and 16:00 h) until visual satiety on a commercial pellet of 35% crude protein (Skretting, Alexandria, Egypt) according to (Algammal et al., 2020). The organic wastes and other debris were siphoned and 30% of the water was replaced daily to reduce the toxicity of ammonia. Fish that showed normal reflexes with no apparent lesions were selected pathogenicity assessment.

Pathogenicity assessment

A total of 180 acclimated Nile tilapia was randomly distributed into twelve concrete tanks, with 15 fish per tank. Each treatment was performed in triplicate. The fish of the first group (C) were injected with 0.5 mls of sterile saline water and served as a control, while the fish of the other groups (T1, T2 and T3) were injected with 0.5 mls of the overnight culture of virulent *C. freundii*, *P. aeruginosa*, and *S. agalactiae* respectively at a concentration of 3×10^7 cells mL^{-1} cultured on tryptic soy broth (Oxoid) at 37 °C for 24 h accordance to (Algammal et al., 2020). The pathological clinical signs and cumulative deaths were recorded daily among experimental groups for two weeks post-treatment. Sample from moribund and freshly dead fish were collected, examined immediately to verify the cause of death.

Statistical Analysis

Statistical analysis was performed using RStudio (v4.2.3) and Microsoft Excel. Chi-square tests assessed survival differences and pathogen distribution across districts, with significance set at $P < 0.05$.

RESULTS

Clinical and postmortem findings of fish collected in cage fish farms

The clinical inspection revealed that most of the infected fish shared the similar clinical signs, including hemorrhages on external body surfaces, mainly at the ventral aspect of the abdomen and around the vent. Others showed fins erosions, skin darkness, ulcers, eye loss, scale loss and detached scales. Internally, the infected fish showed typical signs of hemorrhagic septicemia, pale liver, necrotic gills, and empty gastrointestinal (GIT).

Bacteriological assay

This study identified three key fish pathogens *Citrobacter spp.*, *Pseudomonas spp.*, and *Streptococcus spp.*, across Nyamagana, Rorya, Musoma MC, Sengerema, Musoma DC, and Busega districts. Five non-pathogenic genera were also detected: *Enterobacter spp.*, *Escherichia spp.*, *Pantoea spp.*, *Leclercia spp.*, and other *Enterobacteriaceae*. Pathogenic isolates showed distinct colony morphologies: *Pseudomonas spp.* formed large, irregular, fruity-scented colonies with yellow-green fluorescence on Pseudomonas Agar; *Citrobacter spp.* appeared yellowish, opaque, and round on Tryptic Soy Agar; *Streptococcus spp.* formed small, translucent colonies of non-motile, Gram-positive cocci in chains. *Escherichia spp.*, showed medium, dry, round pink colonies; *Pantoea spp.* had yellow-pigmented, convex colonies on nutrient agar; *Leclercia spp.* formed circular, smooth colonies with variable pigmentation. Other *Enterobacteriaceae* exhibited motile, oxidase-negative, Gram-negative rod morphology typical of facultative anaerobes. Biochemical profiles are summarized in Table 1.

Molecular characterization of bacteria isolates from cage farmed Nile tilapia

Analysis of sequenced 16S rRNA gene confirmed that the 25 bacteria isolates were: *Citrobacter freundii*, *Pseudomonas aeruginosa*, and *Streptococcus agalactiae* (Table 2). In addition, eleven non-pathogenic were identified as *Enterobacter mori*, *Enterobacteriaceae bacterium*, *Pantoea agglomerans*, *Leclercia adecarboxylata*, *Enterobacter ludwigii*, *Pseudomonas geniculate* and *Escherichia coli*. The BLAST results showed percentage identities ranging from 98.29% to 100%, with expected values of 0 for all sequences. Maximum scores ranged from 745 to 1109, while query coverage was 100% for each blasted sequence.

Table 1: Biochemical characteristics of bacterial isolates from cage farmed Nile tilapia

Characteristics	Isolates							
	Pseudomonas sp.	*Aeromonas sp.*	*Streptococcus sp.*	*Psychrobacter sp.*	*Escherichia sp.*	*Enterobacter sp.*	*Pantoea sp.*	*Leclercia sp.*
Gram stain	-	-	+	-	-	-	-	-
Motility	+	+	-	-	+	+	+	+
Catalase	+	+	-	+	+	+	+	+
Oxidase	+	+	-	+	-	-	-	-
NR	+	+	-	-	+	+	+	+
GH	+	+	-	-	-	-	-	-
CU	-	+	-	+	+	+	+	+
MF	+	+	-	-	+	+	+	+
H_2S	-	-	-	-	-	-	-	-
Urease	+	+	-	-	+	-	-	-
Indole	-	+	-	-	+	-	-	-
Methyl red	-	+	-	-	+	-	-	-
VP	-	+	-	-	-	+	+	+

Note: Abbreviations: MR, methyl red; VP, Voges–Proskauer; MF, Mannitol fermentation; CU, Citrate utilization; GH, Gelatin hydrolysis; NR, Nitrate reduction; H_2S, Sulphide

Table 2: BLAST results obtained after comparing the 16S rRNA sequences of isolated bacteria samples from the Lake Victoria cage fish farms, with those in the NCBI database.

Accession number	Bacteria Species	Base pair size	Maximum score	Query cover (%)	E- value	% Identity
PX171350	*P. aeruginosa**	600	1109	100	0.0	100
PX171365	*S. agalactiae**	600	1109	100	0.0	100
PX171334	*C. freundii**	600	811	100	0.0	100
PX171381	*E. mori*	600	745	100	0.0	100
PX171380	*E. bacterium*	600	774	100	0.0	100
PX171385	*P. agglomerans*	600	889	100	0.0	100
PX171386	*L. adecarboxylata*	600	1000	100	0.0	100
PX171384	*E. ludwigii*	600	1064	100	0.0	100
PX171383	*P. geniculate*	600	1064	100	0.0	100
PX171387	*E. coli*	600	1070	100	0.0	100

Note: Isolates indicated with asterisks have been previously reported as fish pathogens.

Distribution of pathogenic bacteria isolated from cage fish farms

The distribution of *P. aeruginosa*, *S. agalactiae*, and *C. freundii* across six cage fish farming districts revealed no statistically significant variation in species proportions (Chi-square test with Monte Carlo simulation: *P. aeruginosa*, p = 0.112; *S. agalactiae*, p = 0.078; *C. freundii*, p = 0.378). However, Poisson regression indicated a significant overall effect of district on total bacterial counts (p = 0.016). Nyamagana district exhibited the highest prevalence of *P. aeruginosa* (42.9%) and *C. freundii* (36.4%), while *S. agalactiae* was most dominant in Musoma MC (40.0%). In contrast, Musoma DC and Sengerema showed minimal bacterial presence (figure 3). Non-pathogenic isolates collectively accounted for a modest proportion of the microbial community (n = 8, 14.3%) (Table 3).

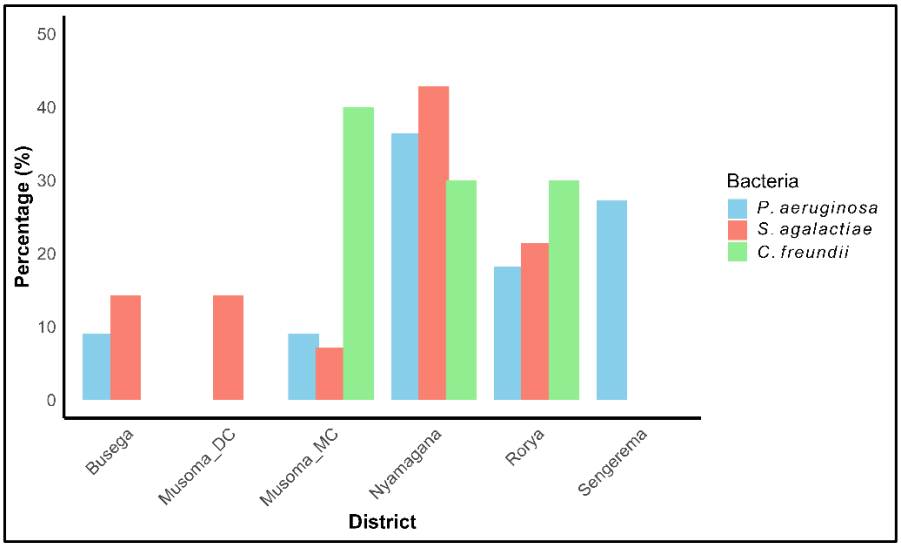

Figure 3: Geographic distribution of pathogenic bacterial species across six districts in LVB

Table 3: Overall Distribution of Bacterial Isolates from Cage Fish Farms (N = 56)

Bacterial Species	N (%)
Pseudomonas aeruginosa	14 (25.0%)
Streptococcus agalactiae	10 (17.9%)
Citrobacter freundii	11 (19.6%)
Enterobacter mori	5 (8.9%)
E. bacterium	1 (1.8%)
Pantoea agglomerans	1 (1.8%)
Leclercia adecarboxylata	1 (1.8%)
Enterobacter ludwigii	1 (1.8%)
Providencia geniculate	1 (1.8%)
Escherichia coli	1 (1.8%)

Pathogenicity assessment

Tanks Water Monitoring

All the tested physical-chemical parameters (total dissolved salts, salinity, temperature pH, and dissolved oxygen) were within the standard range for the production of Nile tilapia in freshwater throughout the challenge trial period (Table 4). There were no significant variations in water parameters in all experimental groups and control group ($p > 0.05$).

Table 4. Tanks water physical–chemical parameters characteristics determined in experimental setup throughout the study period (14 days).

Groups	TDS (mg/L)	S (PSU)	T (°C)	PH	DO (mg/L)
Treatment 1 (*C. freundii*)	23.35 ± 1.4	0.02 ± 0.003	26.89 ± 0.07	8.31 ± 0.1	7.10 ± 0.3
Treatment 2 (*P. aeruginosa*)	27.02 ± 1.4	0.02 ± 0.003	26.74 ± 0.07	7.94 ± 0.1	8.30 ± 0.3
Treatment 3 (*S. agalactiae*)	25.45 ± 1.4	0.02 ± 0.003	26.99 ± 0.07	7.82 ± 0.1	7.40 ± 0.3
Control	30.10 ± 1.4	0.03 ± 0.003	27.08 ± 0.07	7.94 ± 0.1	8.20 ± 0.3
Standard range	<500	0–8	25–32	7–9	5–15

Note: TSD = total dissolved solids; S = salinity; T = temperature; DO = dissolved oxygen; Exp = experiment.

Clinical Signs and Pathological Findings

The clinical signs as well as fish morbidity and mortality were recorded in all experimental groups for two weeks post-challenge. The results demonstrated that the fish of the control group did not reveal any mortalities or pathological lesions, while those of the other groups displaying high mortalities and pathological lesions of hemorrhagic septicemia. Fish exposed to *P. aeruginosa*, showed ragged fin, gill erosion, pectoral fin hemorrhage (Figure 6)., white pectoral fin, redding of the fin that develop to white patches, detached scales and scattered hemorrhagic spots. Those exposed to *C. freundii*, showed skin hemorrhage, fin rot, and skin ulcer which ended up into open sore (Figure 7) while those exposed to *S. agalactiae*, showed scale loss, eye hemorrhage, fin rot (Figure 8a), bulging of the eye, cloudy eye, eye loss, white color to the base of openings and fins, (Figure 8b).

Survival Analysis

Fish challenged with *Pseudomonas aeruginosa* exhibited the lowest survival probability, with rapid mortality observed within the first 10 days. The control group maintained 100% survival throughout the study (figure 4). Survival differences among groups were statistically significant (log-rank test: $\chi^2 = 28.4$, df = 3, $p < 0.001$), with pairwise comparisons confirming significantly reduced survival in the *P. aeruginosa* group compared to all others. No significant difference was observed between *C. freundii* and *S. agalactiae* ($p = 0.3907$). Median lethal time (LT_{50}) was shortest for *P. aeruginosa* (4 days), followed by *C. freundii* (8 days) and *S. agalactiae* (>10 days) (Table 5). Final cumulative mortality at day 14 was 87% for *P. aeruginosa*, 53.3% for *C. freundii*, and 40% for *S. agalactiae* (Table 5). Bacteriological examination confirmed successful re-isolation of *P. aeruginosa*, *S. agalactiae*, and *C. freundii* from skin ulcers and internal organs of dead and moribund fish.

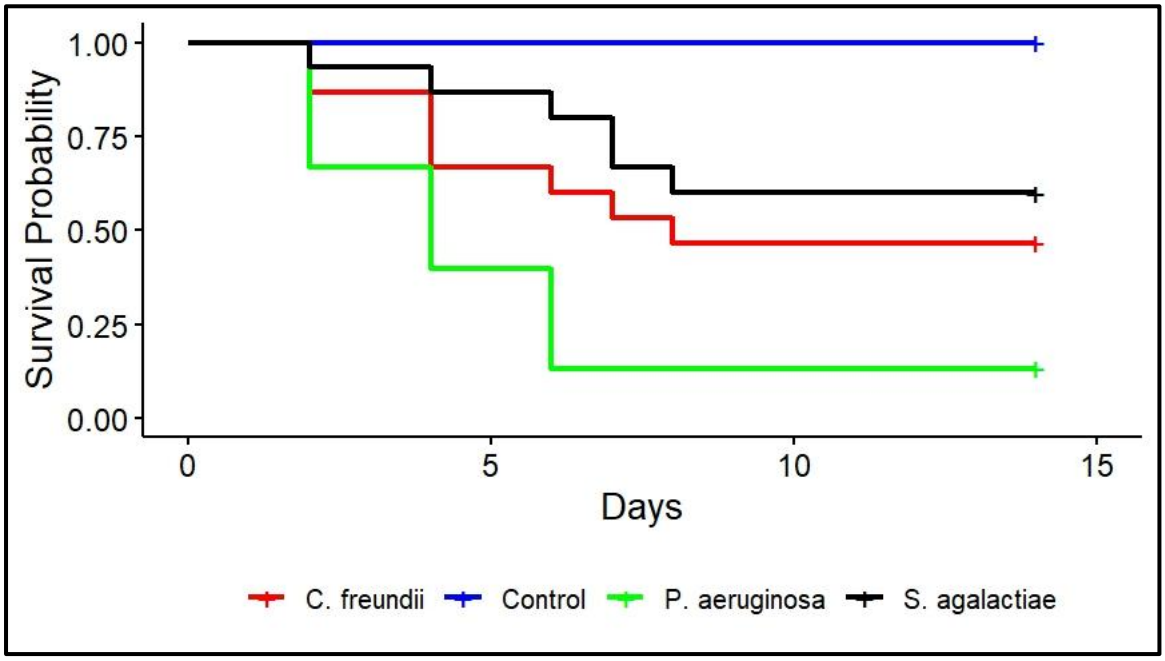

Figure 4: Probability of survival of Nile tilapia inoculated intraperitoneally with 0.5 ml of isolated bacteria at a concentration of 3×10^7cfu ml^{-1} in comparison to control group fingerlings.

Table 5: Mortality outcomes and survival metrics of Nile tilapia (*Oreochromis niloticus*) following 14-day exposure to bacterial pathogens.

Pathogen	Cumulative mortality (%)	LT_{50} (days, 95% CI)	Pairwise log-rank p-value
Control	0	-	Reference
C. freundii	53.3	6 (5–8)	0.0031
S. agalactiae	40	8 (6–>10)	0.0105
P. aeruginosa	86.7	5 (4–6)	<0.001

Phylogenetic analysis

The phylogenetic tree of 16S rRNA gene clustered the analysed sequences together for each species of bacteria whose taxonomic identity is reliable (Figure 5), indicating accurate species identification through the amplified barcode. Similarly, bacteria of the same species clustered together irrespective of their geographical origin (Figure 4) demonstrating strong genetic conservation within bacterial species across sampling sites in cage fish farms within Lake Victoria. This finding suggests that geographical separation has minimal impact on the genetic structure of these bacterial populations.

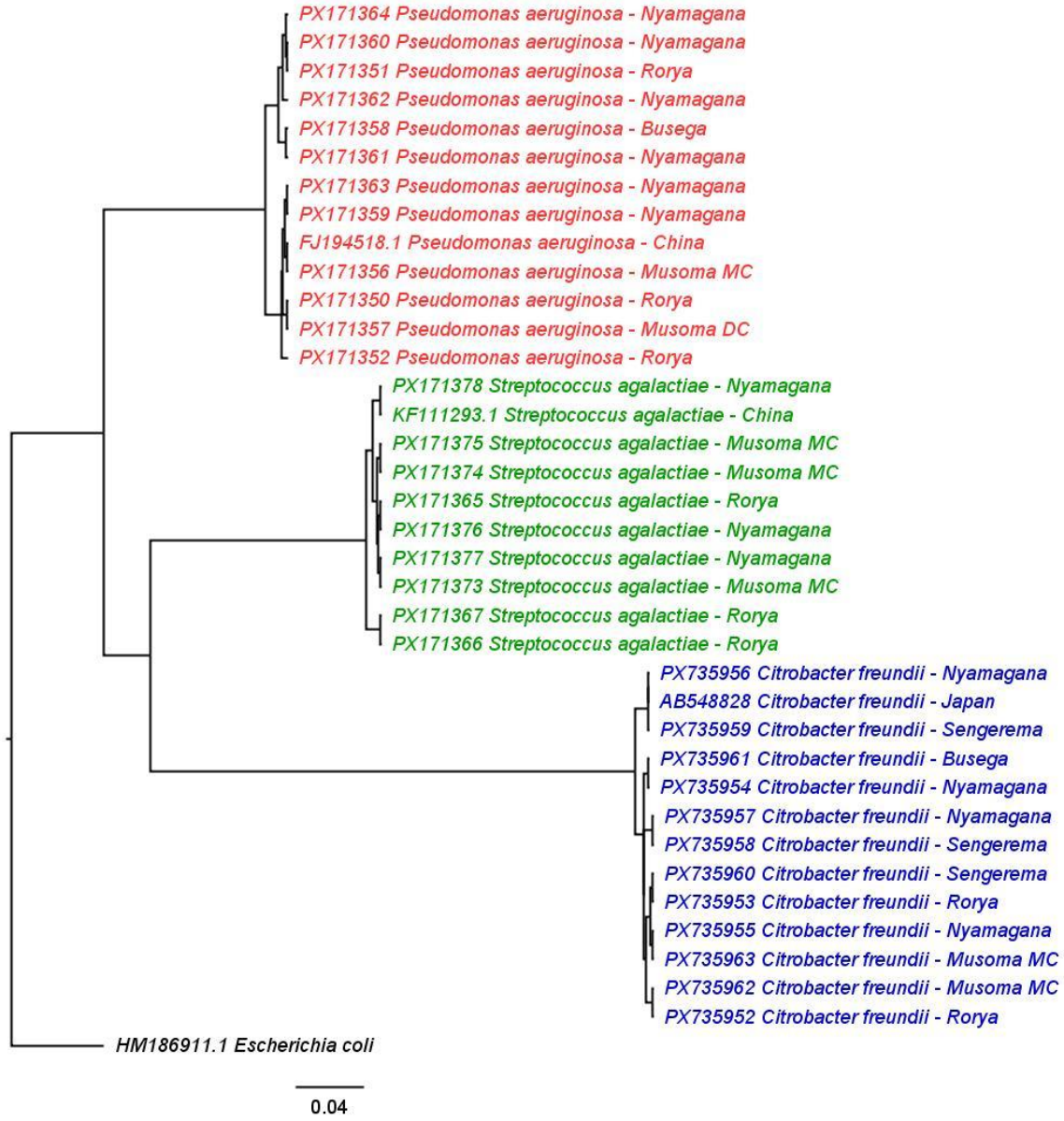

Figure 5. Bayesian phylogenetic tree showing the evolutionary relationships among 16S rRNA haplotypes of pathogenic bacteria isolated from Nile tilapia sampled from cage fish farms in the Lake Victoria.

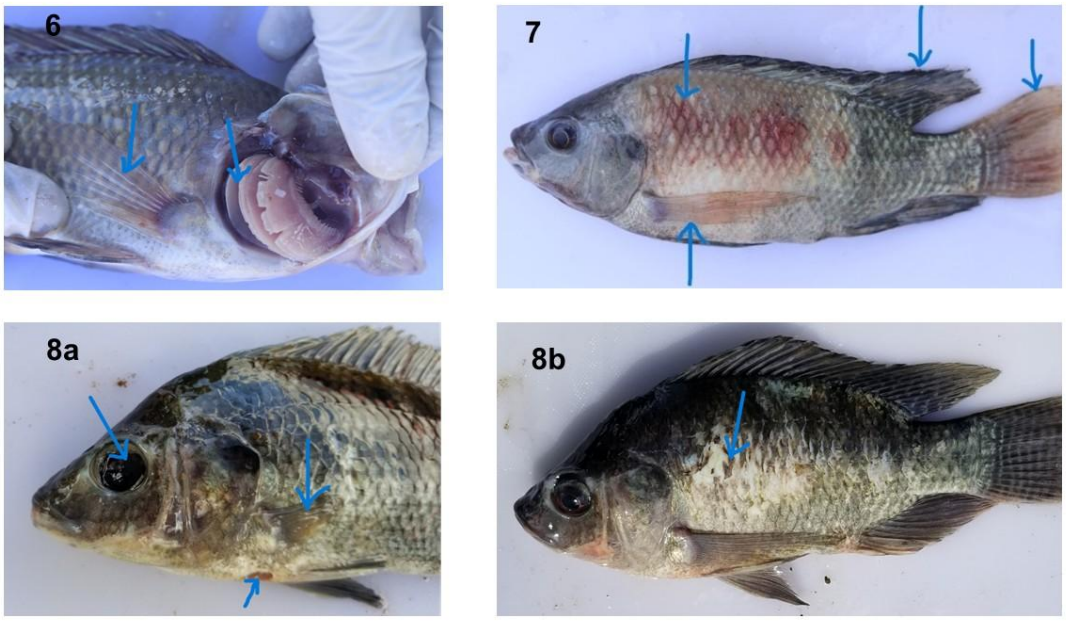

Figure 6: Fish exposed to *P. aeruginosa* showing scattered hemorrhagic spots. **Figure 7:** Fish exposed to *C. freundii* exhibiting ragged fin hemorrhage, skin hemorrhage, and fin erosion. **Figure 8:** Fish exposed to *S. agalactiae* showing (a) scale loss, ulcers, and fin erosion, and (b) eye loss.

DISCUSSION

The study identified *P. aeruginosa*, *C. freundii*, and *S. agalactiae* as the major bacterial species affecting fish in cage fish farms in the LVB, Tanzania. Notably, *P. aeruginosa* was predominantly isolated from Nyamagana, Rorya, Musoma MC, Musoma DC, and Busega, and accounted for 25% of the bacterial isolates, making it the most common pathogen, followed by *C. freundii* (19.6%) and *S. agalactiae* (17.9%). Although descriptive differences in prevalence were observed across districts, chi-square analysis showed no statistically significant variation in species proportions among districts, indicating that these pathogens are broadly distributed throughout the LVB rather than being localized to specific farming areas which is consistent with (Wamala et al., 2018). This finding is further supported by Poisson regression results, which revealed a significant effect of district on overall bacterial abundance but not on individual pathogen dominance.

This high prevalence of *P. aeruginosa* not only confirms earlier findings from cage fish farming but also demonstrates a concerning emergence of *P. aeruginosa* as a dominant threat in Tanzania cage aquaculture marking one of the first molecular confirmations of its dominance in Tanzanian cage farms. This high prevalence aligns with previous studies that reported *P. aeruginosa* as a major contributor to bacterial infections in fish farms, accounting for over 50% of such cases from tilapia and channel catfish cultured in Indonesia (Hardi et al., 2018; Karimi et al., 2022; Wamala et al., 2018). The widespread presence of *P. aeruginosa* in the LVB can be attributed by common risk factors inherent to cage aquaculture, including inadequate biosecurity practices, frequent movement of fish and fingerlings between farms, and the use of similar production systems and cultured species across districts which may promote the persistence and dissemination of opportunistic pathogens such as *P. aeruginosa* within interconnected cage farming networks (Hardi et al., 2018; Wamala et al., 2018). Symptoms observed in fish exposed to *P. aeruginosa* included ragged fins, gill erosion, hemorrhages, and white patches, consistent with findings from previous studies (Haenen et al., 2023; Mohamed et al., 2023). Importantly, *P. aeruginosa* induced the highest mortality rate (86.7%) and the shortest median lethal time (LT_{50} = 5 days), reinforcing its pathogenic potential. These findings align with previous reports describing *P. aeruginosa* as a highly virulent opportunistic pathogen capable of causing rapid systemic infections under stressful rearing conditions (Gołaś et al., 2019; Shams Eldeen et al., 2024).

Citrobacter freundii was isolated in samples collected from all districts except Musoma DC, indicating their widespread prevalence. Infections caused by *C. freundii* are known to result in severe conditions such as haemorrhagic septicaemia, oedema, epizootic ulcerative syndrome (EUS), haemorrhagic enteritis, and red body disease, affecting a variety of finfish species, including common carp, goldfish, eel, catfish, and tilapia which are consistent to this study (Hardi et al., 2018; Sayuti et al., 2021). This marks one of the few reports of *C. freundii* with confirmed pathogenicity in Tanzanian tilapia aquaculture, underlining its emerging significance.

Although *C. freundii* caused significant fish mortality following the pathogenicity assessment (53.3%), the progression of the disease was somewhat slower with a longer LT_{50} compared to *P. aeruginosa*. Its ability to persist across diverse farming environments suggests an adaptive resilience that could complicate future control efforts if left unaddressed.

Streptococcus agalactiae was isolated in 17.9% of the samples and was primarily limited to Musoma MC, Rorya, and Nyamagana. This pattern reflects differences in farm management practices, stocking densities, or fish movement rather than environmental limitation, especially given the absence of significant spatial structuring in the phylogenetic analysis (Pádua et al., 2014). Symptoms associated with *S. agalactiae* infections included scale loss, eye haemorrhage, and fin rot, consistent with other findings which evaluated the clinical and histopathological lesions associated with the bacteria (Ferrari et al., 2024; Noraini et al., 2013; Pretto-Giordano et al., 2010). Despite a lower mortality rate of 40%, over 60% of fish infected with *S. agalactiae* recovered, though often with permanent eye damage. This vision impairment likely affects feeding behaviour, reduces feed efficiency, and contributes to increased feed waste further exacerbating environmental degradation around cage sites (Evans et al., 2004; Noraini et al., 2013). Uneaten feed can further deteriorates water quality, potentially causing economic losses for cage farmers and exacerbating environmental issues (Evans et al., 2004; Noraini et al., 2013). Although *P. aeruginosa* remains the most prevalent and problematic pathogen, this study underscores the multifaceted nature of disease risks in Tanzanian cage aquaculture. Both *C. freundii* and *S. agalactiae* present significant challenges that demand targeted control strategies tailored to their biological behaviours and environmental triggers.

The clustering of *S. agalactiae, P. aeruginosa*, and *C. freundii* isolates into distinct phylogenetic groups across multiple districts suggests the circulation of genetically similar strains a pattern indicative of shared infection sources. These results align with findings from previous studies emphasizing the role of interconnected aquaculture practices and environmental factors in disease transmission. For instance, the genome-based analysis of multidrug-resistant *E. coli* in Lake Victoria (Baniga et al., 2020) illustrated how shared water systems can serve as reservoirs for pathogens, facilitating their dissemination across districts. Similarly, studies on *S. agalactiae*, and *P. aeruginosa* in fish farms in Brazil (Abdallah et al., 2024) and Indonesian (Anshary et al., 2014) reveal the genetic uniformity of strains within localized outbreaks, suggesting common sources of infection, such as contaminated feed, equipment, or water. This study provides molecular evidence that supports the hypothesis of pathogen movement through shared supply chains and water exchange systems among cage farms in the LVB (Barony et al., 2017; Lusiastuti et al., 2013). A particularly novel insight is that despite geographical separation, the pathogens identified in this study do not cluster by district but by species highlighting that the same pathogenic strains are likely being transmitted across multiple farming sites. This points to a pressing need for coordinated regional interventions. Implementation of unified, cross-district biosecurity protocols such as standardized quarantine procedures, improved waste management, and routine pathogen screening could reduce the spread and re-emergence of these bacterial diseases. Moreover, the molecular identification and pathogenicity confirmation of these pathogens provide policymakers and aquaculture managers with crucial data to prioritize resources and inform antimicrobial stewardship programs (Anshary et al., 2014; Baniga et al., 2020). Given the genetic similarity of pathogens across the LVB, individual farm-level interventions are unlikely to be sufficient. Instead, an integrated basin-wide approach could mitigate disease outbreaks more effectively and sustainably.

CONCLUSION

This study revealed the presence of three pathogenic bacteria in cage fish farming systems in Lake Victoria, with *P. aeruginosa* being the most prevalent and problematic pathogen, affecting fish across all sampled districts except Sengerema districts. *Citrobacter freundii* and *S. agalactiae* also pose significant threats, with *P. aeruginosa* causing the highest mortality rates and *S. agalactiae* impairing fish recovery and growth. These pathogens exhibit distinct clinical manifestations, yet collectively contribute to substantial health challenges in the study area. Phylogenetic analysis showed that the clustering of *S. agalactiae*, *P. aeruginosa*, and *C. freundii* isolates into distinct phylogenetic groups across different districts highlights the potential for a shared source of infection among fish farms. These findings emphasize the urgent need for harmonized management practices in the LVB and biosecurity measures in cage fish farming to mitigate the impact of bacterial infections. Strengthening biosecurity protocols, improving water quality, and implementing robust disease monitoring systems are also crucial in reducing pathogen prevalence and their harmful effects. Similarly, routine screening for pathogenic diseases in cage fish farms and hatcheries should be enforced to ensure biosecurity compliance and disease control. Further research should be conducted to track the root

cause of bacterial diseases in the LVB by investigating environmental reservoirs, transmission routes, and the role of wild fish species in pathogen dissemination. Addressing these issues will not only improve fish health but also minimize the economic losses faced by farmers in cage fish farming systems in the Lake Victoria.

FUNDING

This study was supported by the Tanzania Commission for Science and Technology (COSTECH) through the DigiFish project (Digitizing fish-farming value chains for enhanced productivity and food security in the Lake Victoria basin, Tanzania) and The Rufford foundation through the Savecichlids project (grant number- 45091-1). The funder had no say on the design, data collection and analysis, writing of the manuscript and decision to submit the manuscript for publication consideration

CONFLICT OF INTEREST

The author has declared that no competing interests exist.

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