

# Spatial Distribution of Five Myxozoans (Cnidaria: Myxobolidae) Species on the Gills of *Labeobarbus habereri* (Steindachner, 1912) from the Moliwè River, Cameroon

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## Abstract

The distribution of parasites on fish gills is shaped by the organ's structural heterogeneity. This study focuses on the spatial distribution of Myxozoan species on the gills of *L. habereri* in natural conditions, as most known Myxozoan species infect fish gills. The gill apparatus of each host was divided into regions to determine infection site and cyst counts for each parasite species. Data were analyzed at both species and xenocommunity levels, assessing site specificity and comparing mean cyst loads across gill regions. Five cyst-forming Myxozoan species were identified: *Myxobolus paludinosus*, *Myxobolus makombensis*, *Myxobolus nyongana*, *Myxobolus* sp., and *Thelohanellus assambai*. Their prevalence ranged from 14.61% to 98.16%, with mean cyst loads varying between  $7.18 \pm 0.64$  and  $598.56 \pm 29.92$ . No significant differences in epidemiological indices were noted based on the side of the gill. The prevalence of *M. paludinosus*, *M. makombensis*, *Myxobolus* sp., and *T. assambai* was lower in holobranch IV, where cyst accumulation of *M. paludinosus* was also reduced. Epidemiological indices were similar between hemibranchs, except for *M. makombensis*, which showed a higher mean cyst load on the anterior hemibranch. While *M. makombensis* occupied holobranch portions with various patterns, the other Myxozoan species exhibited similar distribution across the gill portions. *Myxobolus paludinosus*, *M. makombensis*, *M. nyongana*, and *T. assambai* developed more cysts in the median gill sector of some holobranchs. This study represents the first analysis of Myxozoan distribution on *L. habereri* gills, highlighting the affinity of certain parasites for specific gill microhabitat.

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## Keywords

Myxozoans, Fish Parasite, Gill, Ecology, Spatial Distribution, Microhabitat

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### 1. Introduction

Myxozoans constitute an economically important group of microscopic metazoan parasites that cause diseases in a wide variety of commercially important fish species [1]. These parasites are distributed worldwide, infecting fish in both marine and freshwater environments [1] [2]. In freshwater ecosystems, myxozoans have complex life cycles involving alternating forms in fish and aquatic oligochaete worms, designated as myxosporean and actinosporean stages respectively [3] [4]. Myxosporeans can infect any organ of the fish body, causing various types of damage [1]. The extent of tissue and organ damage in the host is influenced by biotic factors such as the species of myxozoan, its life cycle stage, infection intensity, and the host's reaction, as well as abiotic factors [5]. Compared to coelozoic species, histozoic myxosporeans are more frequently found to attack the gills [6]. Beyond their pathogenic effects, myxozoans play crucial ecological roles in aquatic ecosystems [1]. As parasites, they regulate fish populations by affecting host survival, growth, and reproduction. Severe infections can lead to mass mortality events, altering community structures and influencing trophic interactions [2] [3]. Despite their widespread presence and ecological importance, myxozoan research remains limited in certain regions, including Cameroon. Studies on the diversity, distribution, and life cycle dynamics of myxozoans in Cameroonian freshwater systems are scarce [5]. The impact of myxozoan infections on local fish species, many of which are critical to artisanal and commercial fisheries, remains poorly understood.

With the increasing interest in fish culture and production, awareness of parasites affecting fish health, growth, and survival has also increased [7]. Cyprinid fish of the genus *Labeobarbus* Rüppel, 1836 are widely distributed in Africa, particularly in the rivers of Cameroon, such as the Moliwè River in Limbé. These fish play a crucial role in river ecosystems and are an important source of sustenance for local communities [8]. *Labeobarbus habereri* (Steindachner, 1912), commonly known as yellow fish, attains a large size and is one of the most economically important fish species in Cameroon. High reproductive capacity, rapid growth, widespread, and commercial acceptance make *L. habereri* a promising species for fish farming in Cameroon.

The popularity of *L. habereri* as a food source reinforces the need for parasitological studies. Understanding the ecological aspects of myxozoan species parasitizing this fish is essential. Disease outbreaks affect the productivity of both natural and artificial aquatic systems, negatively impacting the livelihoods of communities dependent on these resources. Mixed myxozoan infections are common, especially in cyprinid fish [9]. Ecological studies provide information that helps

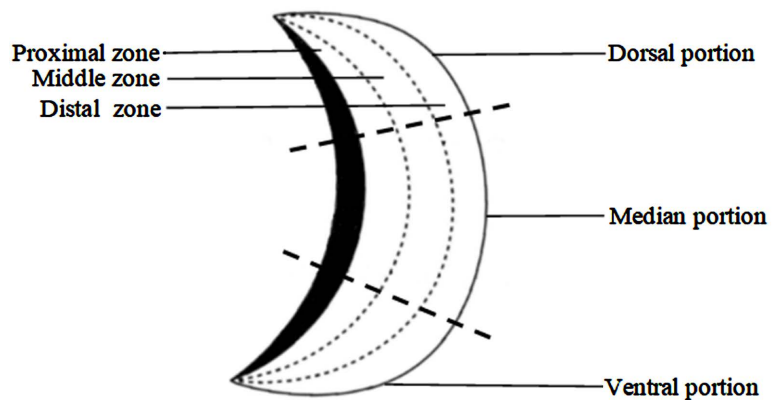
understand how these parasites communities are structured, as well as the processes involved in maintaining their structure [10]. This observation, directly applicable to myxosporean parasites of fish, not only allows for a better understanding of the biology of parasitic species but also helps in developing management strategies.

This study aims to examine the prevalence, mean cyst load, and microhabitat selection determinants of five species of myxosporean found in the gills of *L. habereri* from the Moliwè River in Cameroon.

## 2. Material and Methods

Between March 2018 and February 2020, specimens of *L. habereri* (Family Cyprinidae) were collected from the Moliwè River near the village of Moliwè, adjacent to Limbé in the southwest region of Cameroon. The region exhibits a tropical climate characterized by two main seasons: an extended rainy season from March to November and a dry season from December to February. The Moliwè River is typified by variable water flows, substrates that range from rocky to sandy, and abundant native riparian vegetation. The fish were caught at different sites from coordinates 04° 03' 38.278" N - 09° 14' 45.516" E to 04° 04' 04.328" N - 09° 16' 43.396" E and at these sites, standardized gill nets with predetermined mesh sizes were deployed during peak fish activity periods, either in the early morning or late afternoon, for a fixed duration of 2 - 4 hours. Immediately after capture, specimens were measured, sexed, and preserved in a 10% formalin solution for a minimum of 48 hours prior to dissection.

In the laboratory, prior to identify the exact location of the parasites on the gills, each fish specimen was dissected under an Olympus BO61 stereomicroscope with the aim of extracting the eight (08) holobranchs, each half of which comes from one side (left or right) of the fish's body. Holobranchs were divided arbitrarily following the method of [11] with slight modifications (Figure 1). The holobranchs were individually placed in Petri dishes filled with tap water and numbered I, II, III, and IV in the antero-posterior direction. Each holobranch was further subdivided: the gill filaments were divided into anterior hemibranch (AH) towards the operculum and posterior hemibranch (PH) away from the operculum. Each hemibranch was then subdivided dorsoventrally into ventral portion (VP), median portion (MP), and dorsal portion (DP), based on the number of gill filaments. Additionally, based on the length of the gill filaments, each hemibranch was divided into proximal zone (PZ), middle zone (MZ), and distal zone (DZ). This division resulted in 72 microhabitats per fish side, which were examined under a binocular microscope to search for and count myxozoans cysts. After locating the cysts, some were taken and gently crushed between a slide and coverslip in a drop of water, then examined using a  $\times 100$  objective of an Ivymen light microscope. Myxozoans species were identified following the guidelines of [12]. The number of cysts and their exact locations were recorded for each parasite species.



**Figure 1.** Schematic diagram of an hemibranch showing longitudinal and transversal subdivisions.

Parasite prevalence or infection rate (%), expressed as a percentage, was estimated by dividing the number of *L. habereri* individuals infected with one or more individuals of a particular myxosporean species by the total number of *L. habereri* examined [13]. Mean intensity ( $\bar{x}$ ), as referred to by [13], was calculated as the average number of cysts of a specific myxosporean species found among infected *L. habereri* individuals in the sample, divided by the number of *L. habereri* infected with that myxosporean species. These epidemiological indices were assessed at the microhabitat level using the same approach. To compare prevalence, the chi-square test was employed ( $\chi^2$ ). To compare multiple groups, the Kruskal-Wallis H test was employed, while pairwise comparisons were performed using the Mann-Whitney U test. These non-parametric methods were selected due to their robustness against violations of normality, reduced sensitivity to outliers, and applicability to ordinal or skewed data. This approach provides a reliable framework for assessing differences in central tendency even when the data do not satisfy the assumptions required for parametric tests. All statistical analyses were performed using the SPSS program for Windows version 26.0, with significance set at  $p < 0.05$ .

### 3. Results

Examination of 760 *L. habereri* specimens' gills revealed the presence of *Myxobolus paludinosus* Reed, Basson and Van, 2002; *Myxobolus makombensis* Feudjio-Dongmo, Lekeufack-Folefack, Tene-Fossog, Fomena, Wondji, Yurakhno, Alomar and Mansour, 2022; *Myxobolus* sp., *Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985) Fomena and Bouix, 1997 and *Thelohanellus assambai* Fomena, Marquès, Bouix & Njiné, 1994. Prevalence varied from 14.61% (*T. assambai*) to 98.16% (*M. paludinosus*), while mean cyst load ranged between  $7.18 \pm 0.64$  (*M. nyongana*) and  $598.56 \pm 29.92$  (*M. paludinosus*) (Table 1). At the xenocommunity level, there was no significant difference in infestation rate ( $\chi^2 = 0.001$ ;  $p = 1$ ) or mean cyst load ( $U = 266,129$ ;  $p = 0.17$ ) between the two sides of the host's gill. However, the distribution of myxozoans species was balanced between the left and

right sides of the gill, except for *M. makombensis*, which had a significantly higher average cyst count on the left side (Table 1). Parasite prevalence significantly varied ( $p < 0.001$ ) regardless of the gill side, with the following patterns: *M. paludinosus* > *M. makombensis* > *M. nyongana* > *Myxobolus* sp. = *T. assambai* for the left side, and *M. paludinosus* > *M. makombensis* > *M. nyongana* > *Myxobolus* sp. > *T. assambai* for the right side. Similarly, average cyst accumulation differed significantly ( $p < 0.001$ ) on both gill sides, showing the same distribution pattern on both gill side: *M. paludinosus* > *T. assambai* > *M. makombensis* > *Myxobolus* sp. = *M. nyongana* (Table 1).

### 3.1. Variation of Prevalence and Mean Cyst Load According to Holobranchs

At the xenocommunity level, no significant variation ( $\chi^2 = 1.42$ ;  $p = 0.70$ ) was observed in the proportions of myxozoans species across different branchial arches (Table 2). However, *Myxobolus* sp. and *M. nyongana* parasitized holobranchs equally ( $p > 0.05$ ), while the infestation rates of other species varied significantly in the antero-posterior direction as follows: *M. paludinosus* and *T. assambai* showed I = II = III > VI patterns, and *M. makombensis* exhibited I = II > III = VI (Table 2).

**Table 1.** Epidemiological indices (infection rate and mean cyst load) of myxozoans species between the gill sides.

Parasite species	Left			Right			$\chi^2$ test value		
	$n_1$	%		$n_2$	%				
<i>M. paludinosus</i>	734	96.58 <sup>a</sup>		728	95.79 <sup>a</sup>		0.645		
<i>M. makombensis</i>	579	76.18 <sup>b</sup>		569	74.87 <sup>b</sup>		0.356		
<i>Myxobolus</i> sp.	122	16.05 <sup>d</sup>		124	16.32 <sup>d</sup>		0.019		
<i>M. nyongana</i>	207	26.97 <sup>c</sup>		199	26.18 <sup>c</sup>		0.215		
<i>T. assambai</i>	103	13.55 <sup>d</sup>		93	12.24 <sup>c</sup>		0.586		
<b>Xenocommunity</b>	<b>742</b>	<b>97.63</b>		<b>742</b>	<b>97.63</b>		<b>&lt;0.001</b>		
<b><math>\chi^2</math> test value</b>	<b>1766.14***</b>			<b>1756.47***</b>					
Parasite species	Left				Right				U test value
	$n_3$	$\bar{x}$	$\sigma$	Min - max	$n_4$	$\bar{x}$	$\sigma$	Min - max	
<i>M. paludinosus</i>	734	314.91 ± 15.89 <sup>a</sup>	430.69	1 - 3257	728	295.85 ± 14.76 <sup>a</sup>	398.31	1 - 2906	260.727
<i>M. makombensis</i>	579	21.42 ± 1.75 <sup>c</sup>	42.02	1 - 367	569	16.95 ± 1.52 <sup>c</sup>	36.21	1 - 362	146111.5**
<i>Myxobolus</i> sp.	122	11.79 ± 2.03 <sup>d</sup>	22.47	1 - 119	124	8.37 ± 1.18 <sup>d</sup>	13.18	1 - 54	7300
<i>M. nyongana</i>	207	5.03 ± 0.45 <sup>d</sup>	6.43	1 - 45	199	4.19 ± 0.37 <sup>d</sup>	5.26	1 - 30	18,834
<i>T. assambai</i>	103	40.05 ± 6.67 <sup>b</sup>	67.70	1 - 433	93	39.6 ± 6.96 <sup>b</sup>	39.67	1 - 437	4756
<b>Xenocommunity</b>	<b>742</b>	<b>337.13 ± 15.99</b>	<b>435.49</b>	<b>1 - 3286</b>	<b>742</b>	<b>310.76 ± 14.68</b>	<b>399.87</b>	<b>1 - 2909</b>	<b>265076.5</b>
<b>H test value</b>	<b>864.28***</b>				<b>889.91***</b>				

*M.*: *Myxobolus*, *T.*: *Thelohanellus*,  $n_1$ ,  $n_2$ : number of parasitized individuals;  $n_3$ ,  $n_4$ : number of individuals hosting at least one myxosporean cyst; %: infestation rate;  $\bar{x}$ : mean cyst load;  $\sigma$ : standard deviation; min: minimum value; max: maximum value;  $\chi^2$ : chi-square; U: Mann-Whitney; H: Kruskal-Wallis; \*\*: significant difference at 1% level of confidence; \*\*\*: significant difference at 0.1% level of confidence; identical lowercase letters: non-significant difference for pairwise comparison in the columns; different lowercase letters: significant difference for pairwise comparison in the columns.

Regardless of the holobranchs examined, the infestation rates of myxozoans species significantly varied ( $p < 0.001$ ). For holobranchs I, II, and III, the infestation pattern was noted as *M. paludinosus* > *M. makombensis* > *M. nyongana* > *Myxobolus* sp. = *T. assambai*; whereas for holobranchs IV, it was *M. paludinosus* > *M. makombensis* > *M. nyongana* > *Myxobolus* sp. > *T. assambai* (Table 2). At the xenocommunity level, the cyst accumulation in holobranchs significantly decreased ( $H = 76.46$ ;  $p < 0.001$ ) in the antero-posterior direction. This trend was particularly evident for *M. paludinosus* ( $H = 60.07$ ;  $p < 0.001$ ), with the accumulation model being I = II > III > VI. However, the cyst accumulation of other myxozoans species was statistically similar ( $p > 0.05$ ) across different holobranchs (Table 3).

The mean cyst load varied significantly ( $p < 0.001$ ) among myxozoans species within each holobranch of *L. habereri*. The accumulation model for these parasites' species across the four holobranchs was: *M. paludinosus* > *T. assambai* > *M. makombensis* > *Myxobolus* sp. = *M. nyongana* (Table 3).

**Table 2.** Infection rates of the different myxozoans species on different holobranchs.

Parasite species	Holobranch								$\chi^2$ test value
	I		II		III		IV		
	n	%	n	%	n	%	n	%	
<i>M. paludinosus</i>	728	95.79 <sup>a/A</sup>	728	95.79 <sup>a/A</sup>	723	95.13 <sup>a/A</sup>	698	91.84 <sup>a/B</sup>	16.044 <sup>***</sup>
<i>M. makombensis</i>	533	70.13 <sup>b/A</sup>	505	66.65 <sup>b/A,C</sup>	470	61.84 <sup>b/B,C</sup>	464	61.05 <sup>b/B</sup>	17.979 <sup>***</sup>
<i>Myxobolus</i> sp.	104	13.68 <sup>d</sup>	96	12.63 <sup>d</sup>	87	11.45 <sup>d</sup>	78	10.26 <sup>d</sup>	4.717
<i>M. nyongana</i>	145	19.08 <sup>c</sup>	136	17.89 <sup>c</sup>	147	19.34 <sup>c</sup>	166	21.84 <sup>c</sup>	3.992
<i>T. assambai</i>	97	12.76 <sup>d/A</sup>	90	11.84 <sup>d/A</sup>	81	10.66 <sup>d/A,B</sup>	60	7.89 <sup>e/B</sup>	10.581 <sup>*</sup>
<b>Xenocommunity</b>	<b>738</b>	<b>97.12</b>	<b>740</b>	<b>97.37</b>	<b>734</b>	<b>96.58</b>	<b>733</b>	<b>96.45</b>	<b>1.42</b>
<b><math>\chi^2</math> test value</b>	<b>1826.78<sup>***</sup></b>		<b>1835.33<sup>***</sup></b>		<b>1784.13<sup>***</sup></b>		<b>1720.89<sup>***</sup></b>		

*M.*: *Myxobolus*; *T.*: *Thelohanellus*; n: number of parasitized individuals; %: infestation rate;  $\chi^2$ : chi-square; \*: significant difference at 5% level of confidence; identical letters; \*\*\*: significant difference at 0.1% level of confidence; identical letters: non-significant difference for pairwise comparison; different letters: significant difference for pairwise comparison; capital letters: comparison along the rows; lowercase letters: comparison along the columns.

**Table 3.** Mean cyst load of the different myxozoans species on different holobranchs.

Holobranch		<i>M. paludinosus</i>	<i>M. makombensis</i>	<i>Myxobolus</i> sp.	<i>M. nyongana</i>	<i>T. assambai</i>	Xenocommunity	H test value
		n	n	n	n	n	n	
I	n	728	533	104	145	97	738	806.19 <sup>***</sup>
	$\bar{x}$	186.07 ± 9.03 <sup>a/A</sup>	10.42 ± 0.77 <sup>c</sup>	6.5 ± 0.9 <sup>d</sup>	3.63 ± 0.35 <sup>d</sup>	23.97 ± 3.73 <sup>b</sup>	195.86 ± 9.03	
	$\sigma$	243.61	17.83	9.23	4.18	36.7	245.39	
	Min - max	1 - 29	1 - 137	1 - 44	1 - 32	1 - 218	1 - 35	
II	n	728	505	96	136	90	740	714.71 <sup>***</sup>
	$\bar{x}$	180.99 ± 9.12 <sup>a/A</sup>	12.51 ± 1.16 <sup>c</sup>	7.39 ± 1.15 <sup>d</sup>	2.91 ± 0.33 <sup>d</sup>	28.33 ± 4.65 <sup>b</sup>	191.54 ± 9.09	
	$\sigma$	246.05	26.05	11.29	3.81	44.14	247.54	
	Min - max	1 - 17	1 - 227	1 - 51	1 - 27	1 - 247	1 - 36	

Continued

	<b>n</b>	723	470	87	147	81	<b>734</b>	
III	$\bar{x}$	144.79 ± 7.52 <sup>a/B</sup>	12.05 ± 1 <sup>c</sup>	7.39 ± 1.13 <sup>d</sup>	3.07 ± 0.28 <sup>d</sup>	21.8 ± 4.03 <sup>b</sup>	<b>154.24 ± 7.5</b>	<b>605.57***</b>
	$\sigma$	202.23	21.77	10.58	3.39	36.28	<b>203.77</b>	
	<b>Min - max</b>	1 - 1551	1 - 178	1 - 38	1 - 21	1 - 251	<b>1 - 1594</b>	
	<b>n</b>	698	464	78	166	60	<b>733</b>	
IV	$\bar{x}$	106.89 ± 5.52 <sup>a/C</sup>	9.71 ± 0.89 <sup>c</sup>	5.73 ± 0.98 <sup>d</sup>	3.01 ± 0.26 <sup>d</sup>	19.57 ± 3.72 <sup>b</sup>	<b>110.83 ± 5.37</b>	<b>587.1***</b>
	$\sigma$	145.75	19.36	8.64	3.37	28.81	<b>145.39</b>	
	<b>Min - max</b>	1 - 1052	1 - 211	1 - 32	1 - 19	1 - 154	<b>1 - 1052</b>	
<b>H test value</b>		60.07***	2.4	3.77	7.72	2.79	<b>76.46***</b>	

*M.*: *Myxobolus*; *T.*: *Thelohanellus*; n: number of fish hosting at least one myxozoan cyst;  $\bar{x}$ : mean cyst load;  $\sigma$ : standard deviation; min: minimum value; max: maximum value; H: Kruskal-Wallis; \*\*\*: significant difference at 0.1% level of confidence; identical letters: non-significant difference for pairwise comparison; different letters: significant difference for pairwise comparison; capital letters: comparison along the columns; lowercase letters: comparison along the rows.

### 3.2. Variation of Prevalence and Mean Cyst Load According to Hemibranchs

At the xenocommunity level, the infestation rate between the anterior and posterior hemibranchs showed no significant difference ( $\chi^2 = 2.85$ ;  $p = 0.09$ ), as well as at the specific level ( $p > 0.05$ ) (Table 4).

**Table 4.** Infection rates of myxozoans species on different hemibranchs.

Parasite species	Hemibranch				$\chi^2$ test value
	Anterior		Posterior		
	n	%	n	%	
<i>M. paludinosus</i>	739	97.24 <sup>a</sup>	731	96.18 <sup>a</sup>	1.32
<i>M. makombensis</i>	602	79.21 <sup>b</sup>	571	75.13 <sup>b</sup>	3.59
<i>Myxobolus</i> sp.	122	16.05 <sup>d</sup>	135	17.76 <sup>d</sup>	0.79
<i>M. nyongana</i>	217	28.55 <sup>c</sup>	189	24.87 <sup>c</sup>	2.64
<i>T. assambai</i>	103	13.55 <sup>d</sup>	95	12.5 <sup>c</sup>	0.37
<b>Xenocommunity</b>	<b>750</b>	<b>98.68</b>	<b>741</b>	<b>97.5</b>	<b>2.85</b>
<b><math>\chi^2</math> test value</b>	<b>1824***</b>		<b>1758***</b>		

*M.*: *Myxobolus*; *T.*: *Thelohanellus*; n: number of parasitized individuals; %: infection rate;  $\chi^2$ : chi-square; \*\*\*: significant difference at 0.1% level of confidence; identical lowercase letters: non-significant difference for pairwise comparison within the columns; different lowercase letters: significant difference for pairwise comparison within the columns.

Significant variation ( $p < 0.001$ ) in infestation rates among collected myxozoans species was observed on both the anterior and posterior hemibranchs. On the anterior hemibranch, the infestation model by these species was: *M. paludinosus* > *M. makombensis* > *M. nyongana* > *Myxobolus* sp. = *T. assambai*; whereas on the posterior hemibranch, it was *M. paludinosus* > *M. makombensis* > *M. nyongana* >

*Myxobolus* sp. > *T. assambai* (Table 4). Analysis of the mean cyst load of myxozoans across hemibranchs in *L. habereri* showed statistically identical cyst numbers produced by the xenocommunity between the two hemibranchs (U = 262,304; p = 0.06) (Table 5). Except for *M. makombensis*, all parasites' species exhibited similar results as recorded at the xenocommunity level (p > 0.05). The mean cyst load of *M. makombensis* was significantly higher on the anterior hemibranch (U = 15,350; p < 0.001) (Table 5).

More specifically, the anterior hemibranch of holobranch III (U = 58717.5; p < 0.001) and holobranch IV (U = 56883.5; p = 0.006) were those showing significant high mean cyst load of *M. makombensis* (Table 6). On each hemibranch, significant variation (p < 0.001) was found in the average number of cysts produced by parasites species. The pattern of cyst accumulation by these myxozoans species was consistent across both hemibranchs, with the following distribution: *M. paludinosus* > *T. assambai* > *M. makombensis* > *Myxobolus* sp. = *M. nyongana* (Table 5).

**Table 5.** Mean cyst load of myxozoans species as a function of the hemibranchs.

Parasite species	Hemibranch								U test value
	Anterior				Posterior				
	n	$\bar{x}$	Min	Max	n	$\bar{x}$	Min	Max	
<i>M. paludinosus</i>	739	317.4 <sup>a</sup> ± 15.48	1	3260	731	290 <sup>a</sup> ± 14.85	1	2988	25,680
<i>M. makombensis</i>	602	20.99 <sup>c</sup> ± 1.63	1	383	571	16.47 <sup>c</sup> ± 1.49	1	340	15,350**
<i>Myxobolus</i> sp.	122	9.49 <sup>d</sup> ± 1.5	1	66	135	9.76 <sup>d</sup> ± 1.55	1	98	7944.5
<i>M. nyongana</i>	217	4.62 <sup>d</sup> ± 0.41	1	41	189	4.61 <sup>d</sup> ± 0.39	1	34	20021.5
<i>T. assambai</i>	103	41.26 <sup>b</sup> ± 6.86	1	453	95	37.53 <sup>b</sup> ± 6.42	1	417	4892
<b>Xenocommunity</b>	<b>750</b>	<b>338.1 ± 15.52</b>	<b>1</b>	<b>3334</b>	<b>741</b>	<b>306.5 ± 14.81</b>	<b>1</b>	<b>2992</b>	<b>262,304</b>
<b>H test value</b>	<b>585.313***</b>				<b>600.114***</b>				

*M.*: *Myxobolus*; *T.*: *Thelohanellus*; n: number of fish hosting at least one myxozoans cyst;  $\bar{x}$ : mean cyst load; min: minimum value; max: maximum value; U: Mann-Whitney; H: Kruskal-Wallis; \*\*: significant difference at 1% level of confidence; \*\*\*: significant difference at 0.1% level of confidence; identical lowercase letters: non-significant difference for pairwise comparison within the columns; different lowercase letters: significant difference for pairwise comparison within the columns.

**Table 6.** Mean cyst load of *M. makombensis* among hemibranchs of each holobranch.

Holobranch		Mean cyst load		U test value
		n	$\bar{x}$	
I	AH	433		86321.5
		$\bar{x}$	6.3 ± 0.44	
	PH	410		
		$\bar{x}$	6.89 ± 0.57	
II	AH	426		73,493
		$\bar{x}$	8.34 ± 0.70	
	PH	362		
		$\bar{x}$	7.64 ± 0.79	

Continued

III	AH	n	400	58717.5***
		$\bar{x}$	8.77 ± 0.68	
	PH	n	349	
		$\bar{x}$	6.18 ± 0.58	
IV	AH	n	388	56883.5**
		$\bar{x}$	7.35 ± 0.67	
	PH	n	332	
		$\bar{x}$	4.98 ± 0.49	

AH: anterior hemibranch; PH: posterior hemibranch; n: number of individuals hosting at least one myxozoan cyst;  $\bar{x}$ : mean cyst load; U: Mann-Whitney; \*\*: significant difference at 1% level of confidence; \*\*\*: significant difference at 0.1% level of confidence.

### 3.3. Variation of Prevalence and Mean Cyst Load According to Portions of Holobranchs

Significant differences were found in the exploitation of portions of the gill by the xenocommunity ( $\chi^2 = 8.62$ ;  $p = 0.01$ ) and specifically by *M. makombensis* ( $\chi^2 = 40.87$ ;  $p < 0.001$ ) (Table 7).

*M. makombensis* was found in holobranchs I, III, and IV, with the following distribution pattern: VP > MP > DP. In holobranch II, this parasite species was distributed as follows: VP = MP > DP (Table 8). Other myxozoans species occupied the gill portions equally ( $p > 0.05$ ) (Table 7). Within each portion of the holobranch, there was significant variation ( $p < 0.001$ ) in infestation rates among parasites species. Pairwise comparison tests of infestation rates across all gill portions consistently showed the following pattern: *M. paludinosus* > *M. makombensis* > *M. nyongana* > *T. assambai* = *Myxobolus* sp. (Table 7).

The mean cyst load of the xenocommunity of myxozoans varied significantly ( $H = 74.76$ ;  $p < 0.001$ ) across different portions of the holobranchs. This pattern was consistent ( $p < 0.001$ ) for all parasite's species except for *Myxobolus* sp. ( $p > 0.05$ ). *M. paludinosus* showed significantly higher cyst accumulation in the medial portion and exhibited two distinct patterns of cyst accumulation across portions of holobranchs (Table 9). The first pattern (MP > VP = DP) was observed on holobranch I, II, and III, while the second pattern (MP > VP > DP) was recorded on holobranch IV (Table 10). The mean cyst load of *M. makombensis* differs across portions of holobranchs I, III, and IV, following the model MP = VP > DP. In holobranchs II, it followed the model VP > MP = DP. The mean cysts load of *M. nyongana* was statistically identical ( $p > 0.05$ ) across portions of holobranchs I, II, and IV, but varied significantly ( $p < 0.001$ ) among portions of holobranch III, where it followed the MP > PV = PD model. This pattern was also observed with *T. assambai* in holobranchs II, III, and IV, with mean cyst load statistically similar ( $p = 0.058$ ) across portions of holobranch I (Table 10). Comparison of the mean cyst load of myxozoans species within each portion of the gill revealed significant differences ( $p < 0.001$ ) and three distinct patterns of cyst accumulation.

In the ventral portion, the pattern was *M. paludinosus* > *M. makombensis* = *T. assambai* > *Myxobolus* sp. = *M. nyongana*. The median portion exhibited *M. paludinosus* > *T. assambai* > *M. makombensis* > *Myxobolus* sp. = *M. nyongana*, while the distal portion showed *M. paludinosus* > *T. assambai* > *M. makombensis* = *Myxobolus* sp. > *M. nyongana* (Table 9). The comparison of the average cyst burdens of myxozoans species in each gill section revealed not only highly significant differences ( $p < 0.001$ ) but also three distinct patterns of cyst accumulation. The pattern observed in the ventral section is: *M. paludinosus* > *M. makombensis* = *T. assambai* > *Myxobolus* sp. = *M. nyongana*. The pattern in the median section is: *M. paludinosus* > *T. assambai* > *M. makombensis* > *Myxobolus* sp. = *M. nyongana*. Finally, the pattern in the distal section is: *M. paludinosus* > *T. assambai* > *M. machomen's* = *Myxobolus* sp. > *M. nyongana* (Table 9).

**Table 7.** Infection rates of the myxozoans species among portions of holobranch.

Parasite species	Portion of holobranch						$\chi^2$ test value
	Ventral		Median		Dorsal		
	n	%	n	%	n	%	
<i>M. paludinosus</i>	725	95.39 <sup>a</sup>	737	96.97 <sup>a</sup>	714	93.95 <sup>a</sup>	8
<i>M. makombensis</i>	574	75.53 <sup>b/A</sup>	550	72.37 <sup>b/B</sup>	465	61.18 <sup>b/C</sup>	40.87 <sup>***</sup>
<i>Myxobolus</i> sp.	100	13.16 <sup>d</sup>	124	16.32 <sup>d</sup>	96	12.63 <sup>d</sup>	5.002
<i>M. nyongana</i>	181	23.82 <sup>c</sup>	177	23.29 <sup>c</sup>	166	21.84 <sup>c</sup>	0.89
<i>T. assambai</i>	102	13.42 <sup>d</sup>	97	12.76 <sup>d</sup>	79	10.39 <sup>d</sup>	3.59
Xenocommunity	742	97.63	746	98.16	728	95.79	8.62 <sup>*</sup>
$\chi^2$ test value	1826.37 <sup>***</sup>		1780.37 <sup>***</sup>		1682.86 <sup>***</sup>		

*M.*: *Myxobolus*; *T.*: *Thelohanellus*; n: number of parasitized individuals; %: infection rate;  $\chi^2$ : chi-square test value; \*: significant difference at 5% level of confidence; \*\*\*: significant difference at 0.1% level of confidence; identical letters: non-significant difference for pairwise comparison; different letters: significant difference for pairwise comparison; capital letters: comparison along the rows; lower-case letters: comparison along the columns.

**Table 8.** Infection rate of *M. makombensis* among the portions of each holobranch.

Holobranch		Infection rate			
			VP	MP	DP
		n			
I	n	396	368	282	
	%	52.12 <sup>a</sup>	48.42 <sup>b</sup>	37.11 <sup>c</sup>	
	$\chi^2$ test value	37.41 <sup>***</sup>			
II	n	371	351	252	
	%	48.82 <sup>a</sup>	46.18 <sup>a</sup>	33.16 <sup>b</sup>	
	$\chi^2$ test value	43.67 <sup>***</sup>			
III	n	376	314	258	
	%	49.47 <sup>a</sup>	41.32 <sup>b</sup>	33.95 <sup>c</sup>	
	$\chi^2$ test value	37.74 <sup>***</sup>			

Continued

	n	348	308	244	
<b>Holobranch</b>	<b>IV</b>	<b>%</b>	45.79 <sup>a</sup>	40.53 <sup>b</sup>	32.11 <sup>c</sup>
		$\chi^2$ test value	30.31***		

VP = ventral portion; MP = median portion; DP = distal portion; n: number of parasitized individuals; %: infection rate;  $\chi^2$ : chi-square; \*\*\*: significant difference at 0.1% level of confidence; identical lowercase letters: non-significant difference for pairwise comparison within the columns; different lowercase letters: significant difference for pairwise comparison within the columns.

**Table 9.** Mean cyst load of the myxozoans species across portions of holobranch.

Parasite species	Portion of holobranch												H test value
	Ventral				Median				Dorsal				
	n	$\bar{x}$	$\sigma$	Min - max	n	$\bar{x}$	$\sigma$	Min - max	n	$\bar{x}$	$\sigma$	Min - max	
<i>M. paludinosus</i>	725	164.87 ± 7.92 <sup>a/B</sup>	213.14	1 - 1618	737	295.44 ± 14.91 <sup>a/A</sup>	404.68	1 - 2853	714	153.02 ± 8.26 <sup>a/C</sup>	220.74	1 - 1844	62.54***
<i>M. makombensis</i>	574	15.04 ± 1.09 <sup>b/A</sup>	26.28	1 - 230	550	16.05 ± 1.39 <sup>c/A</sup>	32.59	1 - 287	465	9.86 ± 0.91 <sup>c/B</sup>	19.64	1 - 177	32.776***
<i>Myxobolus</i> sp.	100	6.13 ± 0.96 <sup>c</sup>	9.59	1 - 46	124	7.9 ± 1.18 <sup>d</sup>	13.12	1 - 65	96	9.15 ± 1.61 <sup>c</sup>	15.79	1 - 65	0.976
<i>M. nyongana</i>	181	3.65 ± 0.34 <sup>c/A</sup>	4.64	1 - 34	177	4.58 ± 0.46 <sup>d/A</sup>	6.15	1 - 42	166	2.43 ± 0.18 <sup>d/B</sup>	2.29	1 - 13	13.71***
<i>T. assambai</i>	102	21.27 ± 3.7 <sup>b/B</sup>	3.739	1 - 255	97	43.67 ± 7.58 <sup>b/A</sup>	74.66	1 - 463	79	17.84 ± 2.73 <sup>b/B</sup>	24.3	1 - 152	23.53***
<b>Xenocommunity</b>	<b>725</b>	<b>181.53 ± 8.07</b>	<b>217.32</b>	<b>1 - 1642</b>	<b>737</b>	<b>315.59 ± 15.10</b>	<b>410.05</b>	<b>1 - 3101</b>	<b>714</b>	<b>163.21 ± 8.30</b>	<b>221.91</b>	<b>1 - 1894</b>	<b>74.76***</b>
<b>H tes value</b>	<b>778.23***</b>				<b>895.18***</b>				<b>738.13***</b>				

*M.*: *Myxobolus*; *T.*: *Thelohanellus*; n: number of individuals hosting at least one myxozoan cyst;  $\bar{x}$ : mean cyst load;  $\sigma$ : standard deviation; min: minimum value; max: maximum value; H: Kruskal-Wallis; \*\*\*: significant difference at 0.1% level of confidence; identical letters: non-significant difference for pairwise comparison; different letters: significant difference for pairwise comparison; capital letters: comparison along the rows; lowercase letters: comparison within the columns.

**Table 10.** Mean cyst load of myxozoans species among portions of holobranchs.

Parasite species	<i>M. paludinosus</i>			<i>M. makombensis</i>			<i>M. nyongana</i>			<i>T. assambai</i>		
	VP	MP	DP	VP	MP	DP	VP	MP	DP	VP	MP	DP
<b>n</b>	685	704	661	396	368	282	93	79	68	73	87	58
$\bar{x}$	50.75 ±	90.25 ±	56.22 ±	5.39 ±	6.07 ±	4.22 ±	2.12 ±	2.66 ±	1.78 ±	8.9 ±	14.77 ±	6.72 ±
<b>(min - max)</b>	2.43	4.47	2.78	0.36	0.49	0.36	0.22	0.28	0.15	1.36	2.54	0.97
<b>I</b>	(1 - 519) <sup>b</sup>	(1 - 884) <sup>a</sup>	(1 - 526) <sup>b</sup>	(1 - 62) <sup>a</sup>	(1 - 62) <sup>a</sup>	(1 - 36) <sup>b</sup>	(1 - 13)	(1 - 13)	(1 - 6)	(1 - 70)	(1 - 131)	(1 - 41)
<b>H test value</b>	46.079***			14.63**			5.22			5.696		
<b>n</b>	671	709	648	371	351	252	67	80	62	65	77	56
$\bar{x}$	53.33 ±	89.79 ±	49.88 ±	6.86 ±	6.58 ±	5.79 ±	1.63 ±	2.31 ±	1.65 ±	10.72 ±	17.55 ±	8.96 ±
<b>(min - max)</b>	2.57	4.52	2.77	0.59	0.62	0.61	0.14	0.31	0.18	1.87	2.67	1.49
<b>II</b>	(1 - 470) <sup>b</sup>	(1 - 827) <sup>a</sup>	(1 - 654) <sup>b</sup>	(1 - 77) <sup>a</sup>	(1 - 89) <sup>b</sup>	(1 - 66) <sup>b</sup>	(1 - 9)	(1 - 17)	(1 - 7)	(1 - 80) <sup>b</sup>	(1 - 116) <sup>a</sup>	(1 - 51) <sup>b</sup>
<b>H test value</b>	35.167***			6.71*			2.839			13.776**		
<b>n</b>	662	696	629	376	314	258	87	73	62	66	65	52
$\bar{x}$	43.11 ±	74.38 ±	38.76 ±	5.89 ±	7.41 ±	4.34 ±	1.79 ±	2.86 ±	1.4 ±	7.29 ±	14.63 ±	6.42 ±
<b>(min - max)</b>	2.21	3.96	2.17	0.43	0.64	0.43	0.16	0.34	0.10	1.36	2.99	1.08
<b>III</b>	(1 - 392) <sup>b</sup>	(1 - 828) <sup>a</sup>	(1 - 415) <sup>b</sup>	(1 - 58) <sup>a</sup>	(1 - 80) <sup>a</sup>	(1 - 44) <sup>b</sup>	(1 - 10) <sup>b</sup>	(1 - 18) <sup>a</sup>	(1 - 4) <sup>b</sup>	(1 - 56) <sup>b</sup>	(1 - 159) <sup>a</sup>	(1 - 36) <sup>b</sup>
<b>H test value</b>	40.83***			25.83***			22.285***			13.66***		

## Continued

	N	632	668	574	348	308	244	90	97	63	43	47	35
Holobranch IV	$\bar{x}$	32.35 ±	58.04 ±	26.82 ±	4.99 ±	6.35 ±	3.34 ±	2.22 ±	2.12 ±	1.48 ±	7.95 ±	13.81 ±	5.23 ±
	(min -	1.59	2.95	1.65	0.39	0.66	0.36	0.27	0.17	0.09	1.53	2.67	0.87
	max)	(1 - 237) <sup>b</sup>	(1 - 501) <sup>a</sup>	(1 - 314) <sup>c</sup>	(1 - 51) <sup>a</sup>	(1 - 103) <sup>a</sup>	(1 - 58) <sup>b</sup>	(1 - 15)	(1 - 9)	(1 - 3)	(1 - 49) <sup>b</sup>	(2 - 81) <sup>a</sup>	(1 - 24) <sup>b</sup>
H test value		71.19***			14.64**			3.616			11.61**		

*M.*: *Myxobolus*; *T.*: *Thelohanellus*; VP = ventral portion; MP = median portion; DP = distal portion; n: number of individuals hosting at least one myxozoan cyst;  $\bar{x}$ : mean cyst load; min: minimum value; max: maximum value; H: Kruskal-Wallis; \*: significant difference at 5% level of confidence; \*\*: significant difference at 1% level of confidence; \*\*\*: significant difference at 0.1% level of confidence; identical lowercase letters: non-significant difference for pairwise comparison within the rows; different lowercase letters: significant difference for pairwise comparison within the rows.

### 3.4. Variation of Prevalence and Mean Cyst Load According to Filamentous Zone

At the xenocommunity level, a highly significant difference ( $\chi^2 = 20.439$ ;  $p < 0.001$ ) was observed in the infestation rates of myxozoans across filamentous zones (Table 11). For all myxozoans species recorded, except *T. assambai*, the infestation rate varied significantly ( $p < 0.001$ ) between these zones (Table 11).

**Table 11.** Infection rates of myxozoans species across filamentous zones.

Parasite species	Filamentous zones						$\chi^2$ test value
	Proximal		Middle		Distal		
	n	%	n	%	n	%	
<i>M. paludinosus</i>	731	96.18 <sup>a/A</sup>	737	96.97 <sup>a/A</sup>	673	88.55 <sup>a/B</sup>	57.43***
<i>M. makombensis</i>	454	59.74 <sup>b/C</sup>	555	73.03 <sup>b/A</sup>	493	64.87 <sup>b/B</sup>	30.37***
<i>Myxobolus</i> sp.	20	2.63 <sup>c/C</sup>	70	9.21 <sup>d/B</sup>	151	19.87 <sup>c/A</sup>	121.67***
<i>M. nyongana</i>	260	34.21 <sup>c/A</sup>	15	1.97 <sup>e/B</sup>	4	0.53 <sup>e/C</sup>	513.28***
<i>T. assambai</i>	95	12.5 <sup>d</sup>	102	13.42 <sup>c</sup>	91	11.97 <sup>d</sup>	0.739
<b>Xenocommunity</b>	<b>742</b>	<b>97.63</b>	<b>748</b>	<b>98.42</b>	<b>719</b>	<b>94.61</b>	<b>20.439***</b>
$\chi^2$ test value	<b>1798.55***</b>		<b>2375.77***</b>		<b>1850.08***</b>		

*M.*: *Myxobolus*; *T.*: *Thelohanellus*; n: number of parasitized individuals; %: infection rate;  $\chi^2$ : chi-square; \*\*\*: significant difference at 0.1% level of confidence; identical letters: non-significant difference for pairwise comparison; different letters: significant difference for pairwise comparison; capital letters: comparison along the rows; lowercase letters: comparison along the columns.

Each myxozoans species, with the exception of *M. paludinosus*, exhibited a distinct infestation pattern across the four holobranchs. The infestation profiles across filamentous zones were as follows: ZP = ZM > ZD (in holobranch I and II) and MZ > PZ > DZ (in holobranchs III and IV) for *M. paludinosus*; MZ = DZ > PZ for *M. makombensis*; DZ > MZ = PZ for *Myxobolus* sp.; PZ > MZ = DZ for *M. nyongana* (Table 12). Within each filamentous zone, the infection rate varied significantly ( $p < 0.001$ ) among parasites species. Upon comparing the infection rate, different configurations emerged across the filamentous zones. Specifically,

in the proximal zone, the pattern was *M. paludinosus* > *M. makombensis* > *T. assambai* > *M. nyongana* > *Myxobolus* sp.; in the middle zone, it was *M. paludinosus* > *M. makombensis* > *T. assambai* > *Myxobolus* sp. > *M. nyongana*; and in the distal zone, it was *M. paludinosus* > *M. makombensis* > *Myxobolus* sp. > *T. assambai* > *M. nyongana* (Table 11). A significant difference ( $H = 343.59$ ;  $p < 0.001$ ) was observed in the mean cyst loads of myxozoans species recorded across filamentous zones (Table 13). Except for *Myxobolus* sp., the mean cyst load of all parasite's species varied significantly ( $p < 0.001$ ) between filamentous zones (Table 13). The patterns of cyst accumulation for these myxozoans species between filamentous zones were as follows: PZ = MZ > DZ (holobranchs I to IV) for *M. paludinosus*; DZ > MZ > PZ (holobranchs I to IV) for *M. makombensis*; PZ > MZ = DZ (holobranchs III) for *M. nyongana*; MZ > PZ = DZ (holobranchs I and II), PZ = MZ > DZ (holobranch III), MZ > PZ > DZ (holobranch IV) for *T. assambai* (Table 14). The comparison of the mean cyst load of parasites species within each filamentous zone highlights significant differences ( $p < 0.001$ ) and reveals three different models of cyst accumulation. The pattern recorded in the anterior zone is *M. paludinosus* > *T. assambai* > *M. nyongana* > *M. makombensis* = *Myxobolus* sp.; in the middle zone, it is *M. paludinosus* > *T. assambai* > *M. makombensis* > *Myxobolus* sp. > *M. nyongana*; and in the distal zone, it is *M. paludinosus* > *M. makombensis* = *T. assambai* > *Myxobolus* sp. = *M. nyongana* (Table 13).

**Table 12.** Infection rates of myxosporean species across zones of holobranchs.

Parasite species		Holobranch											
		I			II			III			IV		
		n	%	$\chi^2$ test value	n	%	$\chi^2$ test value	n	%	$\chi^2$ test value	n	%	$\chi^2$ test value
<i>M. paludinosus</i>	PZ	698	91.84 <sup>a</sup>		695	91.45 <sup>a</sup>		671	88.29 <sup>b</sup>		629	82.76 <sup>b</sup>	
	MZ	701	92.24 <sup>a</sup>	170.19 <sup>***</sup>	684	90 <sup>a</sup>	122.36 <sup>***</sup>	681	89.61 <sup>a</sup>	152.24 <sup>***</sup>	670	88.16 <sup>a</sup>	173.65 <sup>***</sup>
	DZ	543	71.45 <sup>b</sup>		556	73.16 <sup>b</sup>		521	68.55 <sup>c</sup>		467	61.45 <sup>c</sup>	
<i>M. makombensis</i>	PZ	266	35 <sup>b</sup>		209	27.5 <sup>b</sup>		195	25.66 <sup>b</sup>		234	30.79 <sup>b</sup>	
	MZ	387	50.92 <sup>a</sup>	41.39 <sup>***</sup>	343	45.13 <sup>a</sup>	64.69 <sup>***</sup>	329	43.29 <sup>a</sup>	75.12 <sup>***</sup>	325	42.76 <sup>a</sup>	28.24 <sup>***</sup>
	DZ	352	46.32 <sup>a</sup>		340	44.74 <sup>a</sup>		344	45.26 <sup>a</sup>		317	41.71 <sup>a</sup>	
<i>Myxobolus</i> sp.	PZ	1	0.13 <sup>c</sup>		10	1.32 <sup>c</sup>		5	0.66 <sup>c</sup>		13	1.71 <sup>c</sup>	
	MZ	35	4.61 <sup>b</sup>	106.69 <sup>***</sup>	35	4.61 <sup>b</sup>	71.38 <sup>***</sup>	27	3.55 <sup>b</sup>	65.73 <sup>***</sup>	29	3.82 <sup>b</sup>	35.16 <sup>***</sup>
	DZ	93	12.24 <sup>a</sup>		85	11.18 <sup>a</sup>		69	9.08 <sup>a</sup>		60	7.89 <sup>a</sup>	
<i>M. nyongana</i>	PZ	143	18.82 <sup>a</sup>		133	17.5 <sup>a</sup>		146	19.21 <sup>a</sup>		166	21.84 <sup>a</sup>	
	MZ	3	0.39 <sup>b</sup>	289.18 <sup>***</sup>	3	0.39 <sup>b</sup>	270.53 <sup>***</sup>	5	0.66 <sup>b</sup>	288.45 <sup>***</sup>	4	0.53 <sup>b</sup>	334.19 <sup>***</sup>
	DZ	1	0.13 <sup>b</sup>		/	/		1	0.13 <sup>b</sup>		2	0.26 <sup>b</sup>	

*M.*: *Myxobolus*; *T.*: *Thelohanelus*; PZ = proximal zone; MZ = middle zone; DZ = distal zone; n: number of parasitized individuals; %: infection rate;  $\chi^2$ : chi-square; \*\*\*: significant difference at 0.1% level of confidence; identical lowercase letters: non-significant difference for pairwise comparison within the columns; different lowercase letters: significant difference for pairwise comparison within the columns.

**Table 13.** Mean cyst load of myxozoans species across filamentous zones.

Parasite species	Zones												H test value
	Proximal				Middle				Distal				
	n	$\bar{x}$	$\sigma$	Min - max	n	$\bar{x}$	$\sigma$	Min - max	n	$\bar{x}$	$\sigma$	Min - max	
<i>M. paludinosus</i>	731	296.04 ± 16.41 <sup>a/A</sup>	443.65	1 - 3426	737	271.82 ± 13.38 <sup>a/A</sup>	363.24	1 - 2604	673	44.27 ± 3.21 <sup>a/B</sup>	83.26	1 - 664	429.07***
<i>M. makombensis</i>	454	5.39 ± 0.35 <sup>d/C</sup>	7.53	1 - 55	555	12.49 ± 1.05 <sup>e/B</sup>	24.73	1 - 258	493	25.69 ± 2.56 <sup>b/A</sup>	56.95	1 - 505	120.66***
<i>Myxobolus</i> sp.	20	2.85 ± 0.61 <sup>d</sup>	2.74	1 - 9	70	7.69 ± 1.89 <sup>d</sup>	15.81	1 - 60	151	12.46 ± 2.19 <sup>c</sup>	26.85	1 - 133	2.57
<i>M. nyongana</i>	260	7.12 ± 0.64 <sup>c/A</sup>	10.36	1 - 75	15	1.27 ± 0.15 <sup>e/B</sup>	0.59	1 - 3	4	1.25 ± 0.25 <sup>e/B</sup>	0.5	1 - 2	23.26***
<i>T. assambai</i>	95	22.28 ± 5.14 <sup>b/B</sup>	50.12	1 - 412	102	44.15 ± 7.45 <sup>b/A</sup>	75.24	1 - 418	91	13.13 ± 2.12 <sup>b/B</sup>	20.23	1 - 117	28.47***
Xenocommunity	742	300.37 ± 16.26	442.85	1 - 3462	748	283.86 ± 13.26	362.66	1 - 2621	719	63.33 ± 3.65	97.86	1 - 664	343.59***
H test value			867.39***				714.66***				146.79***		

*M.*: *Myxobolus*; *T.*: *Thelohanellus*;  $\bar{x}$ : mean cyst load;  $\sigma$ : standard deviation; min: minimum value; max: maximum value; H: Kruskal-Wallis; \*\*\*: significant difference at 0.1% level of confidence; identical letters: non-significant difference for pairwise comparison; different letters: significant difference for pairwise comparison; capital letters: comparison between the rows; lowercase letters: comparison within the columns.

**Table 14.** Mean cyst loads of myxozoans species across filamentous zones.

Parasite species	<i>M. paludinosus</i>			<i>M. makombensis</i>			<i>M. nyongana</i>			<i>T. assambai</i>			
	PZ	MZ	DZ	PZ	MZ	DZ	PZ	MZ	DZ	PZ	MZ	DZ	
I	n	698	701	543	266	387	352	143	3	1	78	90	63
	$\bar{x}$	98.17 ± 5.19 <sup>a</sup>	83.29 ± 3.94 <sup>a</sup>	15.74 ± 1.16 <sup>b</sup>	2.89 ± 0.22 <sup>c</sup>	4.56 ± 0.29 <sup>b</sup>	8.58 ± 0.83 <sup>a</sup>	3.65 ± 0.35	1.33 ± 0.33	1 ± 0	9.15 ± 1.89 <sup>b</sup>	14.3 ± 2.21 <sup>a</sup>	5.14 ± 0.91 <sup>b</sup>
	Min - max	1 - 1088	1 - 687	1 - 222	1 - 28	1 - 39	1 - 102	1 - 32	1 - 2	1 - 1	1 - 116	1 - 95	1 - 40
	H test value		379.39***			35.23***			3.385			16.37***	
Holobranch II	n	695	684	556	209	343	340	133	3	/	62	82	59
	$\bar{x}$	93.32 ± 5.15 <sup>a</sup>	84.57 ± 4.19 <sup>a</sup>	16.29 ± 1.26 <sup>b</sup>	2.78 ± 0.18 <sup>c</sup>	5.91 ± 0.55 <sup>b</sup>	10.91 ± 1.21 <sup>a</sup>	2.95 ± 0.33	1 ± 0	/	11.48 ± 2.58 <sup>b</sup>	17.78 ± 2.29 <sup>a</sup>	6.44 ± 0.99 <sup>b</sup>
	Min - max	1 - 1052	1 - 855	1 - 219	1 - 13	1 - 88	1 - 182	1 - 27	1 - 1		1 - 119	1 - 130	1 - 40
	H/U test value		352.32***			37.14***			78			15.27***	
III	n	671	681	521	195	329	344	146	5	1	52	76	55
	$\bar{x}$	72.82 ± 4.22 <sup>a</sup>	70.61 ± 3.63 <sup>a</sup>	14.05 ± 0.97 <sup>b</sup>	2.79 ± 0.21 <sup>c</sup>	5.22 ± 0.46 <sup>b</sup>	9.88 ± 0.96 <sup>a</sup>	3.05 ± 0.28 <sup>a</sup>	1 ± 0 <sup>b</sup>	1 ± 0 <sup>b</sup>	8.23 ± 2.06 <sup>a</sup>	13.25 ± 2.51 <sup>a</sup>	6.02 ± 0.93 <sup>b</sup>
	Min - max	1 - 867	1 - 679	1 - 183	1 - 17	1 - 48	1 - 155	1 - 21	1 - 1	1 - 1	1 - 99	1 - 129	1 - 26
	H test value		267.83***			54.99***			6.32*			7.81*	

## Continued

	n	629	670	467	234	325	317	166	4	2	34	53	38
	$\bar{x}$	54.31 ± 3.14 <sup>a</sup>	53.11 ± 2.66 <sup>a</sup>	10.41 ± 0.72 <sup>b</sup>	2.34 ± 0.14 <sup>c</sup>	4.38 ± 0.49 <sup>b</sup>	7.99 ± 0.85 <sup>a</sup>	2.95 ± 0.26	1.75 ± 0.48	1.5 ± 0.50	7.74 ± 2.36 <sup>b</sup>	14.17 ± 2.43 <sup>a</sup>	4.21 ± 0.72 <sup>c</sup>
Holobranch IV	Min - max	1 - 579	1 - 425	1 - 95	1 - 15	1 - 100	1 - 110	1 - 19	1 - 3	1 - 2	1 - 78	1 - 74	1 - 18
	H test value	264.38***			51.43***			0.39			20.94***		

*M.*: *Myxobolus*; *T.*: *Thelohanellus*; PZ = proximal zone; MZ = middle zone; DZ = distal zone;  $\bar{x}$ : mean cyst load; min: minimum value; max: maximum value; H: Kruskal-Wallis; \*: significant difference at 5% level of confidence; \*\*\*: significant difference at 0.1% level of confidence; identical lowercase letters: non-significant difference for pairwise comparison within the rows; different lowercase letters: significant difference for pairwise comparison within the rows.

#### 4. Discussion

Examination of the gills of *L. habereri* revealed the presence of five species of myxozoans: *M. paludinosus*, *M. makombensis*, *Myxobolus* sp., *M. nyongana*, and *T. assambai*. According to [14], most known myxozoans species infect the gills, likely because releasing myxospores into the external environment is easier from this organ [15] [16]. The heterogeneous structure of the gills allows myxozoans cysts to develop in the gill filaments, gill lamellae, and the cartilaginous arch. Furthermore, the extensive vascularization of the gills favors the development of histozoic myxozoans species because the capsule formed around the myxozoans plasmodium does not sufficiently inhibit the diffusion of oxygen nutrients to the parasite [17]. [16] Report that myxozoans often infest the gills because they are rich in blood and promote gas exchange. The infestation of the gills by myxozoans is not without effects; [18] report histological changes in the gills due to the presence of myxozoans. These changes include inflammation, hypertrophy of lamellar cells, fusion of neighboring gill filaments, and lifting of the gill epithelium.

Polyparasitism in the gills has previously been reported in Cameroon in *Enteromius martorelli* Roman, 1971 [19], *Ctenopoma petherici* Günther, 1864 [20], and *Schilbe mystus* Linné, 1758 [21]. Occurrence of polyparasitism can be explained by the low parasite densities in natural environments, which leave niches available on the gills of the host fish, facilitating simultaneous infestation by several myxozoans species. Furthermore, multispecies infection does not lead to competition as long as space and resources are sufficient [22] [23].

In *L. habereri*, parasite prevalence ranged from 14.61% to 98.16%, and the mean cyst load varied from 7.18 to 598.56 cysts, confirming the observations of [24] that the epidemiological indices of myxozoans in fish fluctuate significantly in natural environment. Additionally, [25] also notes that the proportion of hosts affected by a parasites species is not fixed and may vary across its geographic range.

Overall, the epidemiological indices of myxozoans species in *L. habereri* did not vary significantly between the left and right side of the gills. The equitable distribution of myxozoans on both sides of the gills has been reported by [10] [20] [21] and [24]. This distribution is likely due to the bilateral symmetry of the gill bio-

tope, which results in similar volumes of water flowing through both sides of the gills [26], ensuring an equitable supply of actinospores to both sides.

This study indicates that the first two to three holobranchs of *L. habereri* are more infected by certain myxozoans species, with *M. paludinosus* cysts accumulating less in holobranch IV. Several authors have also revealed that holobranch IV is the least affected by myxozoans species in Cameroon, they are: [27] for *Myxobolus nyongana* and *Myxobolus njinei* Fomena, Bouix and Birgi, 1935; [20] for *Henneguya pethericii* Fomena, Lekeufack Folefack and Bouix, 2008 and *Myxobolus pethericii* Fomena, Lekeufack Folefack and Tang II, 2007; and [21] for *Henneguya camerounensis* Fomena and Bouix, 1957 and *Henneguya ntondei* Fomena, Lekeufack Folefack and Bouix 2008. The preference for holobranchs I, II, and III is likely due to respiratory water currents and the larger surface area available for colonization [26] [28]. Holobranch IV, being covered by other holobranchs, receives a reduce water current and offers a smaller surface area for actinospores fixation and cyst development.

The distribution of myxozoans on hemibranchs varies according to species, with some preferring the anterior hemibranch of certain arches and others the posterior hemibranch [29]. In this study, *M. makombensis* cysts were significantly more numerous on the anterior hemibranch of holobranchs III and IV, similar to *M. pethericii* in *C. petherici* [20] and *M. nyongana* and *M. njinei* in *Enteromius martorelli* [27]. Conversely, *H. ntondei* had a higher cyst load on the posterior surface of holobranchs I and III in *Schilbe mystus* [21]. Furthermore, [24] also found that, in *Labeo rohita*, *Thelohanellus rohita* mostly affects the posterior hemibranch of all holobranchs. The variability in hemibranchs colonization could be due to changes in gill conformation during the respiratory cycle [30]. The epidemiological indices of other myxozoans species and xenocommunities were similar between the anterior and posterior surfaces of the holobranchs, supporting [21], who observed an equitable colonization of both sides of the holobranchs by *Henneguya camerounensis* and the xenocommunity in *Schilbe mystus*. This equitability appears because the hemibranchs of a holobranchs generally have the same filaments structure and number. [31] affirmed that the type of hemibranch does not significantly influence the developmental capacity of parasites.

Generally, the median portion of the gill was more affected by myxozoans recorded, likely due to the larger surface area provided by more developed gill filaments. Similarly, [20] reported that the median portion of the gills of *Ctenopoma petherici* is more infested by *M. pethericii* and the xenocommunity. Similarly, *M. nyongana* exploits the medial portion of holobranch III in *Enteromius martorelli* [27], and this was attributed to it exposure to the high respiratory water current.

To the best of our knowledge, the unique study dealing with the variation of epidemiological indices of myxozoans on gill filament zone was done by [27], who indicated that *Myxobolus barbi* (syn: *Myxobolus nyongana*) exploits all filamentous zones with mean cyst load decreasing progressively from the distal to the

basal part. In the present study, the infection pattern of the three filamentous zones varied among myxozoans species, likely because the gill system offers different microhabitats, reducing interspecific competition [32] as long as space and resources are sufficient [23]. In addition, [33] suggest that parasite microhabitats vary according to species, developmental stage, host species, and immune response intensity.

Regardless of the fragmentation mode of the gill system, most myxozoans species recorded in *L. habereri* were present in the 72 selected microhabitats, with their epidemiological indices varying significantly from each other. It is likely that all fish examined were exposed to actinospores from the Moliwè River. If exposure begins at the fish's first minute of life [34] and the epidemiological indices vary, therefore the developmental kinetics of these parasites species within the host fish differ significantly. The most critical factor affecting parasite development kinetics is the host's immune response, which varies according to parasite species, target tissue, and host individual [35]. Niche overlap in the spatial distribution of the five species recorded in *L. habereri* suggests a lack of interspecific competition, consistent with observations in other myxozoans species in Cameroon [19] [20] and [21]. This absence of competition can be explained by unsaturated gill niches, likely due to low diversity and low infection levels, as the maximal parasite carrying capacity is rarely reached in natural conditions [36].

## 5. Conclusion

This study revealed five species of myxosporeans with varying prevalence and mean cyst load on the gills of *L. habereri* in the Moliwè River. The distribution of parasites and variations in mean cyst load among different gill microhabitats suggest specific ecological preferences influenced by both biotic and abiotic factors. *Myxobolus paludinosus* emerges as the dominant species, raising concerns about its implications for the management of *L. habereri*. This study emphasizes the necessity of understanding the biology and ecology of myxosporeans to inform resource management and establish disease prevention strategies in the Moliwè River. Therefore, future research should explore the mechanisms behind myxosporean distribution in *L. habereri* by investigating water quality, temperature gradients, and host tissue characteristics influencing microhabitat preferences. Studying the pathogenicity of *Myxobolus paludinosus* and its interactions with the host's immune system can clarify infection thresholds and immune responses. Employing advanced molecular and phylogenetic tools will refine species identification, reveal cryptic species, and elucidate evolutionary adaptations. Establishing long-term monitoring programs in the Moliwè River will uncover seasonal and environmental influences on parasite prevalence. Finally, integrating parasite biology with fisheries management can develop effective disease prevention and sustainability strategies, overall safeguarding local food security. By pursuing these future research avenues, we can better safeguard both fish populations and the livelihoods that depend on them.

## Authors' Contribution

L. F. G. B., A. E. T. T. and N. O. O. A. drafted the proposal, L. F. G. B. and A. E. T. T. participated in the field work and laboratory analysis, L. F. G. B., A. E. T. T. and N. O. O. A. participated in the data analysis and interpretation, F. A. contributed to the correction of the final draft of the manuscript. All authors read, corrected and approved the final manuscript.

## Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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