ABUNDANCE AND MICRO-DISTRIBUTION OF CICHLID FISHES ON A ROCKY SHORE OF LAKE TANGANYIKA

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ABSTRACT Every species of rock dwelling cichlid fishes were counted with help of SCUBA at Luhanga in the northwestern part of Lake Tanganyika in 1980. In this area rocky substrate was prominent especially in shallow bottom, while stone, rubble, gravel or sandy substrates were patchily scattered among rocks. About 7,000 fishes of 38 species were counted in a quadrat (20×20 m^2). Plankton feeders (2 species) were most abundant (56%), omnivores (7 species) and Aufwuchs eater (15 species) composed of 21 and 18%, respectively. Numbers of zoobenthos feeders (8 species) and piscivores including scale eaters (6 species) were about 4%. Plankton feeders were gregarious, while species of the other feeding habits were exclusively distributed to other conspecific individuals. About a half number of species frequented on a specific substrate type as follows: Almost all Aufwuchs eaters preferred strongly on rocks especially in shallow water layer and zoobenthos feeders had different preferences to substrate each other, showing repulsive distribution. Among another half number of species, 3 species adhered to shallow region and the rest species showed ubiquitous distribution without any substrate preference, and their number of individuals was small. It is characteristic that most piscivores (4 species), most omnivores (4 species) and a few zoobenthos feeders (2 species) were ubiquitous. Most species kept a distance from piscivores. Each set of two species of Aufwuchs eater and two species of omnivore often frequented together suggesting a cooperative feeding.

INTRODUCTION

In Lake Tanganyika, cichlids are the most dominant in the littoral fish community (Boulenger, 1898; Poll, 1950, 1953, 1956; Matthes, 1960; Fryer & Iles, 1972; Lowe-McConnell, 1975; Brichard, 1978). The species composition of the littoral fish community differs considerably according to substrate conditions of the habitat, such as muddy, sandy, or rocky bottom (Kawabata & Mihigo, 1982). There are, however, neither detailed quantitative analysis on the fish community in the lake nor studies of the relation between the distribution of each species and substrate conditions.

We carried out a survey on the abundance and distribution of cichlid fishes with respect to micro-habitat on a rocky shore near Uvira at the northwestern end of the lake, from Oct., 1979 to Feb., 1980. This paper presents the results of the census and a synopsis of the relationship between the species' distribution and structure of habitat. Although some references are made to the effects of interspecific relations on the distribution pattern of each species, a more detailed analysis of this for each genus or trophic group has been reported elsewhere (Yamaoka, 1982).

STUDY AREA AND METHODS

The study was carried out on Luhanga shore at the northwestern end (3°31'S, 29°09'E) of

Lake Tanganyika. The shore is located 10–14 km south of Uvira, Zaire, and is mostly covered with rocks. The general description of the area can be found in Kawabata & Mihigo (1982).

A quadrat (20 × 20 m^2) was placed on the lake bottom from the shore line down to a depth of about 11 m. It was further divided with string into 400 small quadrats (1 × 1 m^2). The depth at every intersection of strings was measured with a bathymeter and tapeline. The light intensity on the upper and lateral rock surfaces was measured with a photometer at 50 points at various depths on a fine afternoon (2:00–2:30 p.m. on March 8, 1980). Macrophytic vegetation was entirely lacking in this quadrat.

A detailed map of the bottom was made with the help of SCUBA from mid-October to late December, 1979. All rocks and rubble larger than 10 cm were mapped on semitransparent plastic sheets. To make the mapping accurate, photograph of every small quadrat was taken from an overlooking angle by 35 mm camera (NIKONOS) with 15 mm wide lens.

In order to standardize the substrate description, some criteria for the size of substrate components was adopted (Table 1). Using the bottom map and photographs, a detailed substrate map was made on which every 10 × 10 cm^2 mesh of bottom surface was classified into 6 substrate types. Then each small quadrat was classified into one of the 6 substrate types according to the most abundant substrate type in each.

Table 2 summarizes the census methods and dates. A separate census was made for 4 species-groups from early Jan. to late Feb., 1980. This was done 1 to 3 times by either direct counting in every small quadrat, or by recording on the map the position of adult fish, depending on the fish group. Each census took 4 to 8 hours of diving, sometimes extending over 2 days by one person observing in the same species-group throughout the work. For every species except *Lamprologus brichardi*, every adult fish was classified by sight into 3 size classes. For *L. brichardi*, the most abundant species, adult fish in every small quadrat were counted 3 times and the median value was adopted. *Ophthalmochromis nasutus* and *O. ventralis* could not be discriminated from each other in counting.

Table 1. Size criteria for substrate types and the area covered by the substrates in the quadrat.

Substrate type	Symbol	Diameter of substrate component (cm)	Area in the quadrat (m^2)	(%)	No. of small quadrats	(%)
Rock	Ro	≧50	202.1	(51.9)	231	(57.8)
Stone	St	≧20	61.9	(15.9)	44	(11.0)
Rubble	Ru	≧3	96.2	(24.7)	99	(24.8)
Gravel	Gr	≧0.5	10.2	(2.6)	8	(2.0)
Sand	Sa	<0.5	18.4	(4.7)	18	(4.5)
Mud	Mu	fine as stirred up	0.6	(0.2)	0	(0.0)

Table 2. Summary of census methods and dates for 4 species-groups.

Species	No. of times	Date	Records
Julidochromis spp., *Lamprologus* spp. except for *L. brichardi*, and *Telmatochromis* except for *T. bifrenatus*	3	Jan. 8 Feb. 1* Feb. 16	Position of every individual on the bottom map
L. brichardi	3	Jan. 9 Feb. 2 Feb. 23 & 24	No. of individuals in every small quadrat
T. bifrenatus	1	Feb. 1 & 2	ditto
Species of other genera	2	Jan. 17 & 19 Feb. 16 & 22	ditto

**Julidochromis* spp. and *Telmatochromis* spp. were not censused.

The distribution of each species was analyzed with respect to the substrate. Members of the first species-group were related to the substrate type of mesh on which the fish was recorded, while those of the latter 3 species-groups were related to the substrate type of the small quadrat concerned.

Based mainly on Poll (1956) and Takamura (unpublished), all the species concerned were classified into 6 feeding-habit groups, i.e., Aufwuchs eaters, omnivores, plankton feeders, zoobenthos feeders and piscivores including scale eaters (Table 4). In this paper Aufwuchs eater means a species that feeds exclusively or predominantly on epilithic algae. Though Takamura (unpublished) treated *Limnotilapia dardennei* and *Telmatochromis bifrenatus* as Aufwuchs eaters, the species were regarded as omnivore in this paper from his data of stomach content analysis and Poll (1956)'s data. *Tanganicodus irsacae* was treated as an Aufwuchs eater based on Takamura (unpublished), though Poll (1956) and Liem (1979) regarded it as an omnivore and zoobenthos feeder, respectively.

The differences of bathymetrical or substrate-specific distribution pattern of each species among census times or among size classes were examined with Wilcoxon rank sum test when comparing two sets of data, and with Kruskal-Wallis test when comparing more than three sets of data. The difference in density of each species between areas of every depth or substrate type was examined with Kolmogorov-Smirnov one sample test.

Lloyd (1967) proposed a parameter called 'mean crowding',

$$\mathring{m} = \sum x(x-1)/\sum x,$$

where x is the number of individuals of a species in each quadrat. The parameter shows the mean number of other individuals for an individual per quadrat. The parameter $\mathring{m}+1$ shows the mean number of individuals for an individual per quadrat, which was termed 'mean demand' (Lloyd, 1967). Lloyd (1967) also devised an extended parameter to show the 'interspecies mean crowding'

$$\mathring{m}_{12} = \sum x_1 x_2/\sum x_1$$

showing the mean crowding on species 1 by species 2. Iwao (1976) pointed out that the mean demand can be a more general measure of concentration in both continuous and discrete distribution, and proposed the term 'mean concentration' (symbolized by $\mathring{c}$). The interspecies mean concentration ($\mathring{c}_{12}$) can be called the mean concentration on material 1 by material 2 (Iwao, 1977). Iwao (1977), using the parameter $\mathring{c}_{12}$, devised an index of spatial correlation, ω. The value of ω changes from its maximum, 1 for complete overlap through 0 for independent occurrence, to the minimum, -1 for complete exclusion. In this paper $\mathring{c}$, $\mathring{c}_{12}$, and ω were used to detect the intra- and interspecies distribution pattern as well as to analyze the distribution pattern of every substrate type. Furthermore, $\mathring{c}_{12}$ was extended to determine the total influence of every mean concentration, i.e., $\mathring{m}_1+\sum \mathring{c}_{1i}$ is the inclusive mean concentration, showing the number of other individuals of the same and other species for an individual of species 1 per quadrat.

RESULTS AND DISCUSSION

Structure of Habitat

Figs. 1 and 2 give an over- and sectional topographic views of the observation quadrat, respectively. A zonation of substrate parallel to the shore is prominent. Along the shore a number of large rocks are piled. At the depth of 1–2 m, a gently-sloping bottom forms a shelf composed mainly of rocks interspersed with small area of other substrate types. This region is called the upper shelf. From 2 m depth, a steeply-sloping bottom composed mainly of stones

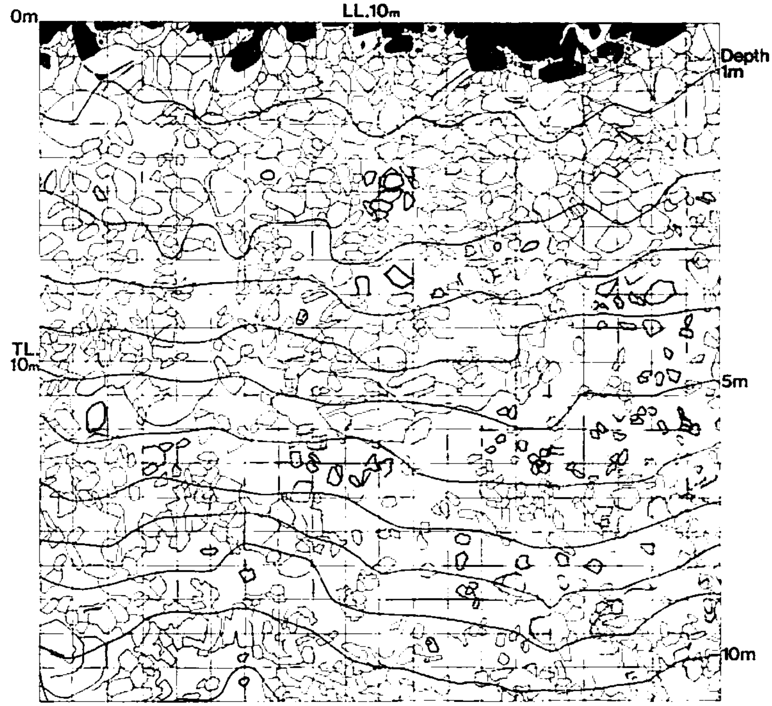

Fig. 1. Bottom map of observation quadrat showing disposition of rocks and depth. Upside denotes shore and solid area is exposed part of rocks to air. LL, longitudinal line; TL, transverse line.

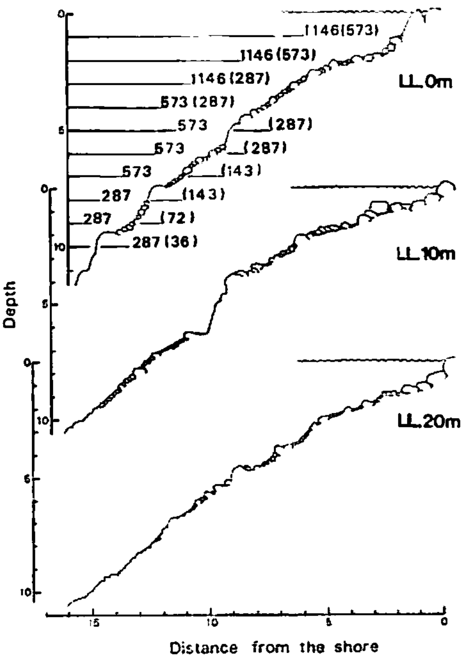

Fig. 2. Sectional topographic views and mean brightness on the bottom at every 1 m depth in the observation quadrat. Three longitudinal lines (LL. 0, 10, 20 m) are shown. The numerals without and within parentheses denote the mean brightness (candle/m^2) on the upper and lateral rock surface, respectively.

Table 3. Adjoining ratio of small quadrats (A) and mean concentration within a small quadrat (B) of own and between any two substrate types. The former is the ratio of adjoining frequency to the expected value of random distribution. The latter is shown as a percentage of the whole area (1 m^2), and the column m gives the percentage of the mean area to the total area of the quadrat (400 m^2).

(A) Substrate type	Ro	St	Ru	Gr	Sa
Rock	1.30				
Stone	0.84	1.63			
Rubble	0.47	1.20	2.24		
Gravel	0.63	0.89	0.80	9.86	
Sand	0.69	0.54	0.41	1.44	6.66

(B) Substrate type	m	$\overset{*}{c}$	$\overset{*}{c}_{12}$ Ro	St	Ru	Gr	Sa
Rock	51.9	69.4	—	10.7	13.8	1.6	3.5
Stone	15.9	25.8	36.7	—	29.7	2.5	4.2
Rubble	24.7	43.0	30.7	19.2	—	2.8	3.4
Gravel	2.6	13.4	32.5	15.1	26.3	—	11.1
Sand	4.8	24.4	37.8	13.4	16.8	5.9	—

and rubble extends toward the deepest end of the quadrat (Appendix 1). This region is called the lower slope. The texture of zonation is often interrupted by a rocky cliff. Stones and rubble are piled on the upper side of the cliff making a gentle ridge. Sandy and gravelly substrates surround the foot of the cliff making a gentle ravine.

The upper shelf received much sunlight but is wavy, probably formed by the action of the wave itself. The scarcity of substrate types other than rocks on the upper shelf may also be attributed to the wave action.

Since mud was rare (Table 1), it was included in the sand in the following analysis. Table 3 shows the distribution pattern of every substrate type within and among small quadrates. Each substrate type tends to be concentrated within 1 m^2, suggesting they were in patches. Since the adjoining ratio with the same substrate type is higher than 1, the patch is likely to extend over 1 m^2.

Between stones and rubble and between gravelly and sandy substrates, both the degrees of concentration and adjoining are high, but not between rocks and stones and between rubble and gravelly substrates. Thus, the substate does not change gradually in space, but patches of three major substrate types, i.e., rock, stone-rubble, and gravelly-sandy substrate extend more or less discretely. However, since rocks are abundant, patches of other types are scattered among the rocks.

Abundance and Distribution of Cichlid Fishes

Thirty-eight species of cichlid were found at census times. Appendix 1 tabulates the census records in relation to the depth of water. In each species the difference in the total number of fish between census times was small. The total number of fish of all the cichlid species was about 7,000 and the average per m^2 was about 18.

The number of individuals varied greatly from species to species. The most numerous group was plankton feeders and they accounted for 56% of fish found in the area (10.2 fish/m^2). The second most numerous group was the omnivores (21%, 3.8 fish/m^2). Aufwuchs eaters was the third (18%, 3.3 fish/m^2). Each of the zoobenthos feeders and piscivores composed only about 2% of all the fish (0.4 fish/m^2).

None of the species showed significant differences in bathymetrical and substrate-specific distribution pattern between census times. Therefore, for every species the data of two or three census times were combined.

Table 4 shows that all the species can be divided into 4 groups depending on whether or not the density differed according to the depth and substrate type.

In groups I and II, the density was significantly different according to the depth. Among

Table 4. Results of the statistical tests for differential distribution of every species according to the depth and substrate type (A) and differential distribution pattern among size classes (B), and the region and substrate on which the species adheres. Major feeding habit is also shown. Results are shown as significantly different at a 1% level (++), at a 5% level (+), or insignificant at a 5% level (−). The slash denotes the absence of available data. Up: upper shelf: Low: lower slope; A: Aufwuchs eater; B: zoobenthos feeder; O: omnivore; Pi: piscivore; and Pl: plankton feeder.

		Result of test						
		Depth of Water		Substrate				
Group	Species	(A)	(B)	(A)	(B)	Region	Substrate type	Feeding habit
I	*Asprotilapia leptura*	++	−	++	−		Ro	A
	Eretmodus cyanostictus	++	−	++	−	Up	Ro	A
	Lamprologus furcifer	++	+	++	−		Ro	B
	Petrochromis polyodon	++	++	++	++		Ro	A
	Simochromis curvifrons	++	−	++	−	Up	Ro	A
	Simochromis diagramma	++	−	++	−	Up	Ro	A
	Telmatochromis bifrenatus	++	++	++	−		Ro & Sa	O
	Tropheus moorei	++	+	++	−		Ro	A
	Lamprologus lemairei	++	+	++	−	Low	St	Pi
	Lamprologus savoryi	++	−	++	−	Low	St & Ru	Pl
	Lamprologus toae	++	−	++	−		St	B
	Telmatochromis temporalis	+	++	++	+		St & Ru	A
	Lamprologus brichardi	++	/	++	/	Low	Ru	Pl
	Lamprologus callipterus	++	−	++	−		Ru	B
	Xenotilapia sp.	++	−	++	−	Low	Sa	O
II	*Haplochromis pfefferi*	++	−	−	−	Up		O
	Tanganicodus irsacae	++	−	−	−	Up		A
	Telmatochromis caninus	++	−	−	−	Up		B
III	*Lamprologus modestus*	−	++	++	−		Gr & Sa	B
	Lamprologus tretocephalus	−	−	++	−		Ru	B
IV	*Julidochromis marlieri*	+	−	−	−			O
	Julidochromis transcriptus	−	+	+	−			O
	Lamprologus compressiceps	−	++	−	−			B
	Lamprologus elongatus	−	++	−	−			Pi
	Lamprologus leleupi	−	−	−	−			B
	Lamprologus profundicola	−	−	−	−			Pi
	Limnotilapia dardennei	−	−	−	−			O
	Lobochilotes labiatus	−	+	−	−			O
	Ophthalmochromis spp.	−	+	−	−			A
	Perissodus microlepis	−	++	−	−			Pi
	Perissodus straeleni	−	−	−	−			Pi
	Simochromis marginatus	+	−	−	−			A
	Petrochromis famula	−	−	−	−			A
	Petrochromis fasciolatus	−	−	−	−			A
	Petrochromis orthognathus	−	+	−	−			A
	Petrochromis trewavasae	+	−	−	−			A

them, some Aufwuchs eaters and one zoobenthos eater, *T. caninus*, were limited to the upper shelf, which may be called the upper shelf species. The number of individuals in every upper shelf species was small. Most of the zoobenthos feeders preferred the lower slope. A piscivore, *L. lemairei*, and plankton feeders were limited to this region (lower slope species).

Some species showed a differential distribution pattern in depth among size classes. In all these species except *Telmatochromis* spp., younger individuals tended to be distributed over the shallower region (Appendix 1). These species is sure to go to or spread over deeper bottom as they become larger without changing their preferred substrate type.

Since almost all the species of groups I and III did not show differential distribution pattern in substrate type among size classes, substrate type looked more influential than depth in the micro-distribution of these species. Nevertheless, the distribution of the upper shelf and lower slope species seemed to be determined by some vertically changing factors because their occurrences were sharply limited to one region in spite of the presence of any substrate type on the other region.

For every species in groups I and III, the significantly preferred substrate types were determined using an F-test at a 1 % level (Appendix 2), and the result is summarized in Table 4. When preferring a particular substrate, most Aufwuchs eaters preferred rocks. This substrate type gives a wide feeding site to these fishes. Zoobenthos feeders preferred various substrate types. *L. toae* rarely took food in the daytime while the other zoobenthos feeders often took food during the same period. This species seemed to prefer stones as a resting site. On a similar evidence, a piscivore, *L. lemariei*, also seemed to prefer stones as a resting site. Plankton feeders preferred stones and/or rubble. *L. brichardi* seemed to prefer rubble as a resting site since this species fed in open water more than 1 m from the bottom. An omnivore, *Xenotilapia* sp. searched food by plunging its snout into the sand.

Some species preferred two successive substrate types, but none of them favored rock-stone or rubble-gravel substrates. This was a parallel phenomenon to the substrate structure as mentioned before, which suggests that these species selected their habitats according to the discontinuity of substrate components. Though *T. bifrenatus* frequented on rocks as well as on sand, it is probable that they adhered to sand deposited on and between rocks.

The species in group IV may be called ubiquitous with respect to depth and substrate types. It is characteristic that zoobenthos feeders were relatively few, while many omnivores and most piscivores were included in this group. Concerning every ubiquitous Aufwuchs eater, the number of individuals was smaller than that of any rock-preferring Aufwuchs eater other than upper shelf species (Appendix 1).

Intra- and Interspecific Relationships in Distribution Pattern

The value of mean concentration ($\mathring{c}$) for every species and spatial correlation (ω) was calculated for every species combination within a group and between group IV and the other groups, using the data from small quadrats on Feb. 16 and 22. For *T. bifrenatus* and *L. brichardi* the data of Feb. 16 and Feb. 1 and 2 were used, respectively. Only the results for the species of more than 10 individuals are tabulated in Appendix 3.

The values of $\mathring{c}$ indicate that *L. brichardi* was distributed most densely where it inhabited. *T. bifrenatus* was the second most dense. In addition, *A. leptura*, *L. savoryi*, and *T. temporalis* showed values higher than 2, showing that these species are likely to aggregate or even if they are territorial the territory is much smaller than 1 m^2. Among the rest except the ubiquitous species, abundant species were thought to be exclusive for conspecific individuals. Kawanabe (1981), Yamaoka (1982) and Takamura (unpublished) have shown that *T. moorei* and *P. polyodon* have a territory of about 1 m^2.

Between two species of different groups other than those shown in Appendix 3, the value of ω must be much smaller than 0, because a species preferred one substrate type which was avoided by another. In Appendix 3 the value of ω was much smaller than 0 between one of the piscivores and most other species. The two species censused on different days, *L. brichardi* and *T. bifrenatus*, showed no spatial correlation to piscivores. These indicate that most species kept a respectful distance from these piscivores. The upper shelf looked hard to utilize even for ubiquitous species except *L. dardennei* and *Ophthalmochromis* spp.

In other combinations, the value of ω was, in general, between 0 to -1, suggesting that most species are distributed independently from other species, are exclusive to some of others, or tend to select a more subtle difference in quality of habitat. Concrete examples of each will be reported for Aufwuchs eaters by Takamura (unpublished).

A very high spatial correlation was found between two omnivores, *Lobochilotes labiatus* and *Limnotilapia dardennei*, and between two Aufwuchs eaters, *P. polyodon* and *T. moorei.* For the latter combination, Takamura (unpublished) suggested a symbiotic relationship in feeding. A similar relationship is expected for the two omnivores.

Rather high spatial correlations were seen among *L. furcifer*, *A. leptura* and two *Julidochromis* spp. and among rock-preferring Aufwuchs eaters except *A. leptura.* Since the number of *L. furcifer* was low in spite of preferring rocks and since *A. leptura* and *Julidochromis* spp. often shared the highly negative values of ω with other rock-preferring species, these species are

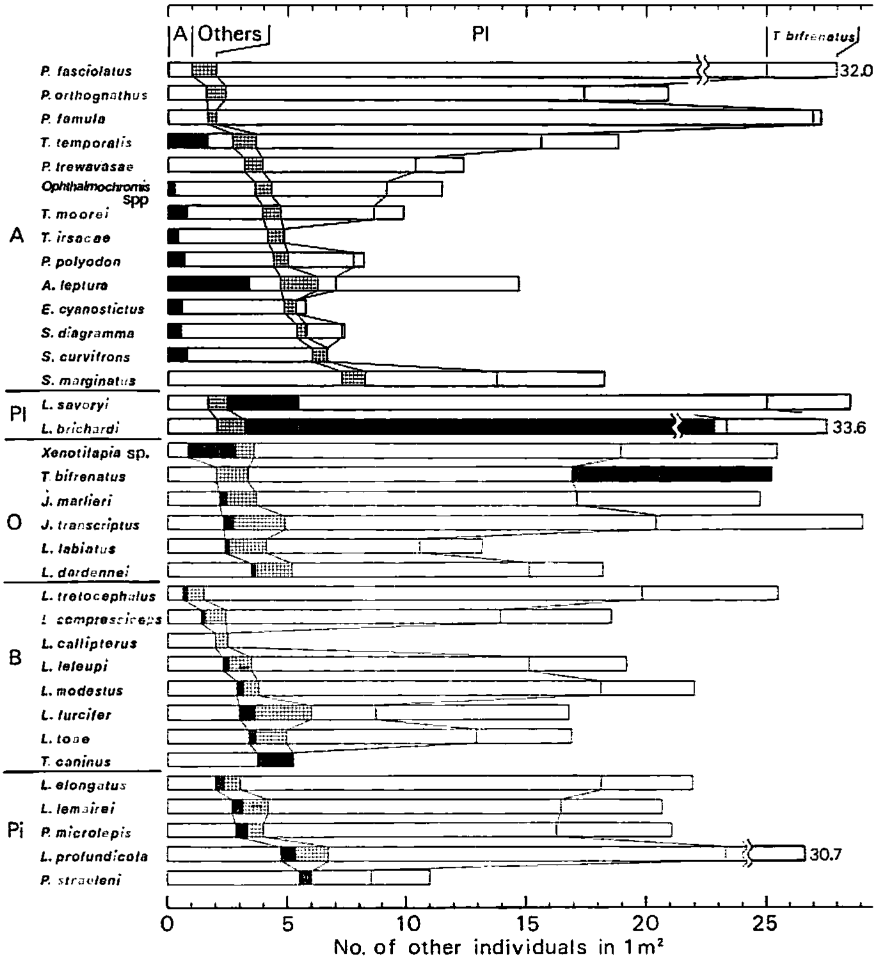

Fig. 3. Inclusive mean concentration for every species. The value is shared by three groups of different feeding habits and *T. bifrenatus*. The solid bar shows the mean concentration of conspecific individuals. Others consists of zoobenthos feeder, piscivore, and omnivore except *T. bifrenatus*. Other symbols are the same as Table 4.

sure to adhere together to some specific quality of rock surface. The rock-preferring Aufwuchs eaters except *A. leptura* seemed to comprise another set of species in which every species favored the same kind of quality of rock surface. They concentrated together on rocks as a feeding site, and shared competitive interspecific relationships (Takamura, unpublished). For example, *T. moorei* aggressively excludes members of the related species, *Simochromis* spp., from its feeding site, and *P. polyodon* does so for members of congeneric species, while these aggressive species are relatively tolerant to members of unrelated species. A similar relationship is expected between the two *Julidochromis* species.

To understand the interspecific relationships from another aspect, the exclusive mean concentration of every species was compared (Fig. 3). Rock-preferring Aufwuchs eaters except *A. leptura* frequented area less crowded with fish of different feeding habits. The dominant species had a lower degree of concentration, probably because of their own aggressiveness, and subordinate species were forced to feed in more crowded areas. Upper shelf species of Aufwuchs eater frequented the less crowded but wavy area near the shore, which seemed hard to utilize for other Aufwuchs eaters. Some ubiquitous Aufwuchs eaters such as 4 spp. of *Petrochromis* and *T. temporalis*, frequented low concentration areas with those with the same feeding habit but were crowded with those with other feeding habits.

Plankton feeders and most omnivores had a high degree of concentration. Their feeding does not seem to be affected strongly by other individuals of the same and other species. The degree of concentration for zoobenthos feeders varied from species to species, which may be attributed to their species–specific substrate selection. *L. profundicola* and *P. straeleni* seemed less threatening to other species as compared with other piscivores.

The distribution pattern of each rocky shore cichlids must reflect their feeding habits, manner of habitat utilization, and intra- and interspecific relationships. Takamura (unpublished) and Yamaoka (1982) have already suggested that interspecific interaction strongly affects the distribution pattern of Aufwuchs eaters. Our results confirm this and also show that zoobenthos feeders tend to scatter according to their species-specific habitat preference. Dominant piscivores may disturb the distribution pattern of other species around them. The present paper also suggests that the vertical texture and substrate composition of the rocky shore must be responsible for distribution and abundance of each species.

ACKNOWLEDGEMENTS We wish to express our heartful thanks to Délégue Général and other members of the I.R.S. (Institut de Recherche Scientifique) of Zaire, especially Director Menga Kuluki Kwetuenda, Mr. Ngabo Mihigo and all other staff of the I.R.S./Uvira Station, for their official and private support during our stay at Uvira.

This study would not have been possible without the generous advice and cooperations of the following people during the survey in Lake Tanganyika; Professor Hiroya Kawanabe and Mr. Nseu Bekeli Mbomba, Kyoto University, Professor Masakazu Kawabata, Shizuoka Women's College, and Mr. Yuji Ankei, Yamaguchi University. We also give heartful thanks to them.

The study was partly supported by the Grant-in-Aid for Overseas Scientific Survey (Nos. 404130, 504328, 56041032 and 57043028) from the Ministry of Education, Science and Culture, Japan.

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Appendix 1. Census results of each size class each time for every species and the area of each substrate type in every 1 m depth of water. S: small sized fish, M: middle sized fish, L: large sized fish.

depth	time	*L. brichardi*	*L. savoryi*				*L. calliptorus*				*L. compressiceps*			
			S	M	L	T	S	M	L	T	S	M	L	T
0–1	1st										2			2
	2nd											1		1
	3rd													1
1–2	1st								3	3		1		1
	2nd							1	3	4		2		2
	3rd							1		1				
2–3	1st	26	1			1					1	2		3
	2nd	33							1	1	1	1		2
	3rd	25							1	1		2		2
3–4	1st	148	2	1	2	5								
	2nd	243		2	2	4						1		1
	3rd	192	2	2	4	8						2		2
4–5	1st	428		1	3	4					1			1
	2nd	675		1	2	3						1		1
	3rd	545		3	1	4								
5–6	1st	773	7	5	5	17								
	2nd	969	5	11	5	21						1		1
	3rd	981	5	11	4	20					1			1
6–7	1st	671	7	7	3	17								
	2nd	650	2	7	4	15						1		1
	3rd	762	6	10	11	27					2			2
7–8	1st	487	2	3	1	6								
	2nd	361	2	6	3	11						1		1
	3rd	560	2	5	2	9					1			1
8–9	1st	444	1	2	1	4								
	2nd	445	1	2	4	7								
	3rd	419	2		3	5							1	1
9–10	1st	438		4	1	5								
	2nd	431		6	2	8								
	3rd	532	1	3	4	8								
10–11.1	1st	232		3	3	6						2	1	3
	2nd	248		2	4	6							1	1
	3rd	300		1	4	5						1	2	3
Total	1st	3,647	20	26	19	65			3	3	4	5	1	10
	2nd	4,055	10	37	26	73		1	4	5	1	9	1	11
	3rd	4,316	18	35	33	86		1	1	2	5	5	3	13
Size			S	M	L	T	S	M	L	T	S	M	L	T

depth	time	*L. furcifer*				*L. leleupi*				*L. modestus*				*L. toae*			
		S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T
0–1	1st		2		2		2		2		3		3			1	1
	2nd		1		1	1	1		2		1		1				
	3rd		1		1	1	2	1	4								
1–2	1st			1	1	3	2	3	8	2	6	1	9				
	2nd			1	1		2	2	4		8	1	9				
	3rd			1	1	1	3	3	7	3	8		11				
2–3	1st					3	1	1	5	2	1		3	1			1
	2nd			1	1	1	1	1	3	1	2		3				
	3rd						1		1	1	1		2		1		1
3–4	1st		1		1	1	3		4	2	2	1	5	2	1	4	5
	2nd					1	2	1	4		1	2	3		3	4	7
	3rd		1	1	2		1	2	3		1	1	2	2		2	4
4–5	1st	2	1	1	4		6	2	8	3	1	3	7	2		3	5
	2nd			6	6	1	3	3	7		4	4	8			1	1
	3rd	2	1	7	10	2	2	3	7		4	2	6			1	1
5–6	1st		2	1	3		3	3	6			6	6			1	1
	2nd		1	1	2	4	2	4	10			2	2			1	1
	3rd		1		1	4	1	2	7		1	4	5	1			1
6–7	1st						4	4	8			3	3				
	2nd					1	3	1	5			2	2				
	3rd					1	2	2	5		1	4	5				
7–8	1st		1		1	1	1		2			1	1				
	2nd			1	1		1	1	2		2	1	3				
	3rd		1		1	1			1		1	2	3				
8–9	1st							1	1		2	1	3				
	2nd					1	1	1	3			2	2				
	3rd							1	1	1	5	2	8				
9–10	1st						1		1		1	1	2				
	2nd						1	2	3			2	2				
	3rd						2	2	4			1	1				
10–11.1	1st	1	2	1	4		1		1		2	1	3				
	2nd		3	1	4		1	1	2		1	1	2				
	3rd		2	2	4			2	2			2	2				
Total	1st	3	9	4	16	8	24	14	46	9	18	18	45	5	1	9	15
	2nd		5	10	15	10	18	17	45	1	19	17	37		3	6	9
	3rd	2	8	11	21	10	14	18	42	6	21	18	45	2	2	3	7
Size		S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T

depth	time	*L. tretocephalus*				*L. elongatus*				*L. fasciatus*				*L. lemairei*				*L. profundicola*			
		S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T
0–1	1st					3			3												
	2nd					1			1												
	3rd					1			1												
1–2	1st		2		2	7	1		8												
	2nd		1		1	3		1	4												
	3rd		1		1	4			4												
2–3	1st						4	1	5										1		1
	2nd	1			1		1	1	2												
	3rd					1	1	3	5					2		1	3				
3–4	1st	1		1	2									2	1		3				
	2nd	1			1		2		2					1	3	2	6		1		1
	3rd			1	1		1		1		1		1	1	3	1	5				
4–5	1st		2		2											1	1				
	2nd		1	1	2		3		3						2	2	4			1	1
	3rd		1	1	2	1			1							3	3		1	1	2
5–6	1st		2	1	3			4	4												
	2nd	5	3	2	10		1		1										1		1
	3rd	1	1	2	4	2		3	5												
6–7	1st	4		1	5																
	2nd	1	3		4			4	4										1	1	2
	3rd		2		2			5	5										1		1
7–8	1st	1	1		2			1	1							1	1				
	2nd	2	1		3			1	1							2	2		1		1
	3rd	2	3		5		1	2	3							1	1				
8–9	1st	2		3	5			3	3												
	2nd	4		3	7			2	2												
	3rd	2	1	1	4																
9–10	1st		4	2	6			2	2												
	2nd			1	1		1		1										2		2
	3rd	1	1	2	4	1		6	7										1	1	2
10–11.1	1st		1	1	2			1	1						2		2		1		1
	2nd		1	2	3		1		1						1		1				
	3rd			1	1			2	2							1	1		1		1
Total	1st	10	10	9	29	10	5	12	27				0	2	3	2	7		2		2
	2nd	13	10	9	32	4	9	9	22				0	1	6	6	13		5	2	7
	3rd	9	8	8	25	10	3	21	34		1		1	3	3	7	13		5	2	7
Size		S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T

Appendix 1. (continued)

depth	time	A. leptura				E. cyanostictus				H. pfefferi				Ophthalmochromis spp.				S. curvifrons			
Size		S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T
0–1	1st		4	2	6		6	31	37										7	5	12
	2nd		2	3	5		4	16	20					3	3		6	2	9	7	18
1–2	1st			11	11		1	4	5		3	1	4								
	2nd			3	3		1	3	4					8	5		13	1	3		4
2–3	1st			3	3			1	1												
	2nd							2	2					2	3	2	7				
3–4	1st	1		5	6																
	2nd			5	5									1	1		2				
4–5	1st	1		1	2																
	2nd	4			4										2	1	3				
5–6	1st	3		3	6																
	2nd	5	1	3	10																
6–7	1st																				
	2nd																				
7–8	1st		1		1																
	2nd	2			2										1	1	2				
8–9	1st		2		2																
	2nd															1	1				
9–10	1st		3	2	5																
	2nd	1	1		2										2		2				
10–11.1	1st	18	1	10	29																
	2nd	2	9	8	19																
	1st	23	11	37	71		7	36	43		3	1	4						7	5	12
	2nd	15	13	22	50		5	21	26				0	14	17	5	56	3	12	7	22

depth	time	S. diagramma				S. marginatus				T. caninus				T. temporalis				T. irsacae			
Size		S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T
0–1	1st	2	7	2	11		2	1	3	1	1	1	3	8	35	13	56		4	4	8
	2nd	1	11	3	15					3	1		4	8	45	5	58		1	5	6
1–2	1st			1	1		3	2	5			1	1	43	102	31	176		2	3	5
	2nd						2		2					35	70	22	127		3	1	4
2–3	1st													32	64	7	103		1	1	2
	2nd													37	36	10	83				
3–4	1st							1	1					36	41	15	92				
	2nd													26	37	2	65				
4–5	1st							1	1					30	73	16	119				
	2nd							1	1					16	49	8	73				
5–6	1st													30	36	3	69				
	2nd			1	1									15	29	3	47				
6–7	1st													13	19	8	40				
	2nd													2	18	5	25				
7–8	1st													16	15	5	36				
	2nd													13	18	7	38				
8–9	1st													15	18	7	40				
	2nd													25	15	2	42				
9–10	1st													35	16	13	64				
	2nd							[illegible]	1					21	19	7	47				
10–11.1	1st													14	16	1	31				
	2nd													16	15	3	34				
	1st	2	7	3	12		5	5	10	1	1	2	4	272	435	119	826		7	8	15
	2nd	1	11	4	16		2	2	4	3	1		4	214	351	74	639		4	6	10

depth	time	T. moorei				P. famula				P. fasciolatus				P. orthognathus			
Size		S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T
0–1	1st	27	32	50	109									1			1
	2nd	7	26	40	73												
1–2	1st	6	22	63	91	1	1	1	3	1	1		2		1		1
	2nd	5	18	42	65	1			1						1		1
2–3	1st	15	11	14	40	1			1					1			1
	2nd	5	9	8	22												
3–4	1st	2	8	9	19		1		1					1			1
	2nd		7	4	11					1			1	1			1
4–5	1st	1	2	12	15										2		2
	2nd		5	6	11		1		1								
5–6	1st			6	6												
	2nd		3	8	11										1		1
6–7	1st		1	5	6			1	1							1	1
	2nd							1	1								
7–8	1st		3	2	5		1		1							1	1
	2nd															1	1
8–9	1st			5	5											2	2
	2nd			2	2										1	2	3
9–10	1st			5	5										1	3	4
	2nd			2	2											1	1
10–11.1	1st			3	3										1	1	2
	2nd			2	2												
	1st	51	76	172	299	2	3	2	7	1		1	2	3	5	8	16
	2nd	17	71	116	204	1	1	1	3		1		1	1	3	4	8

Appendix 1. (continued)

depth	time	P. polyodon				P. trewavasae				J. marlieri				J. transcriptus				L. dardennei			
Size		S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T
0–1	1st	47	11	3	61	5	4		9		1		1						1		1
	2nd	46	8	2	56	1	2		3	1	1		2						2		2
1–2	1st	7	23	10	40		13		13		1	2	3		2	1	3		3		3
	2nd	3	11	5	19	3	7	1	11			1	1					1	2		3
2–3	1st		4	1	5	1	8	1	10	1		1	2		1		1				
	2nd		4		4		4	1	5		2	1	3	1	2		3		1		1
3–4	1st		2		2	1	2	1	4	1	1	1	3		1	1	2		1		1
	2nd		4	1	5					1	1	2	4					1	1		2
4–5	1st		1	1	2			1	1	1	4	3	8	1	1		2		1		1
	2nd		1	3	4			1	1		2	2	4		2		2		1		1
5–6	1st		2	2	4		1	1	2	2	1	3	6	2	5		7		3		3
	2nd		3		3			3	3	1	2	4	7		1	3	4		1		1
6–7	1st			1	1			3	3	3	2		5		3		3				
	2nd							1	1		2	1	3		1	1	2				
7–8	1st							4	4		4	1	5	1	2		3				
	2nd							2	2		3		3	1		1	2		2		2
8–9	1st							4	4						1		1		1		1
	2nd										2	1	3	1	1		2		1		1
9–10	1st							3	3	1	2	2	5		1		1		1		1
	2nd							1	1	1		2	3	1	2	1	4				
10–11.1	1st							1	1	2	1	4	7	5	3	1	9		3		3
	2nd							1	1	5	6	1	12	2			2				
	1st	54	43	18	115	7	28	19	54	11	17	17	45	13	20	3	36		14		14
	2nd	49	31	11	91	4	13	11	28	9	21	15	45	6	9	6	21	2	11		13

depth	time	L. labiatus				Xenotilapia sp.				P. microlepis				P. straeleni				T. bifrenatus			
Size		S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T
0–1	1st	7	1		8					4	1		5							1	1
	2nd		3		3					3	1		4			2	2				
1–2	1st	4	1	1	6					11	7	1	19					2	1	4	7
	2nd	1	1		2					3	5		8		1		1				
2–3	1st	1	1		2					2			2					13	19	6	38
	2nd		1		1																
3–4	1st	2			2					2	2		4					46	42	13	101
	2nd	1	1		2						1	3	4								
4–5	1st	1			1					3	5	1	9					79	74	44	197
	2nd	1			1					1	3	1	5								
5–6	1st									2	6		8					22	51	27	100
	2nd		1		1						6	4	10								
6–7	1st		1		1						5		5					41	52	33	126
	2nd						1		1		8		8								
7–8	1st		2	1	3			1	1	1	8	2	11					45	49	42	136
	2nd		2		2					8	5	3	16								
8–9	1st		1		1						12		12					91	70	39	200
	2nd		1		1			1	1		4		4								
9–10	1st		1		1			1	1	3	14	1	18					136	84	45	265
	2nd										6	4	10								
10–11.1	1st					4			4	1	19	2	22					150	72	27	249
	2nd		1		1	2	1	1	4		2	3	5			1	1				
	1st	14	9	2	25	4		2	6	29	79	7	115				0	625	514	281	1,420
	2nd	2	12		14	2	2	2	6	15	41	18	74		1	3	4				

Area of substrate type (m²)

depth	Ro	St	Ru	Gr	Sa	Ma	Total
0–1	36.0	4.7	2.7				43.4
1–2	34.8	10.1	19.2	2.6	0.8		67.5
2–3	12.4	8.6	13.4	0.8	0.1		35.3
3–4	12.2	7.0	9.6	1.2	0.7	0.1	30.8
4–5	16.2	5.2	10.9	1.1	1.4	0.1	34.9
5–6	11.4	6.2	16.2	1.0	1.5	0.3	36.6
6–7	11.2	7.5	10.2	1.3	2.4	0.1	32.7
7–8	14.6	4.2	4.5	0.4	2.0		25.7
8–9	15.1	3.8	3.9	0.2	2.9		25.9
9–10	22.0	2.6	4.0	0.3	2.7		31.6
10–11.1	16.3	2.0	1.7	1.2	3.8		25.0
	202.2	61.9	96.3	10.1	18.3	0.6	389.4
	51.9%	15.9	24.7	2.6	4.7	0.2	100.0

Appendix 2. The number (N) and percentage (%) of individuals occurred on each substrate type for every species censused and result of *F*-test comparing with the percentage of the substrate type. ++, significant at 1% level; +, at 5% level; and –, insignificant at 5% level. N>S and N<S denote the percentage of occurrence is larger than that of the substrate type and *vice versa*.

Substrate	%	N % F-test	N % F-test	N % F-test	N % F-test	N % F-test	N % F-test
		L. savoryi	*L. callipterus*	*L. compressiceps*	*L. furcifer*	*L. leleupi*	*L. modestus*
Ko	51.9	48 19.0 ++ N<S		13 38.1	49 92.6 ++ N>S	72 53.3	40 30.5 ++ N<S
St	15.9	86 35.4 ++ N>S	1 9.1 -	9 26.5	4 7.4 -	29 21.6	20 15.3 -
Ru	24.7	107 44.1 ++ N>S	8 81.8 ++ N>S	11 32.7		27 20.0	37 28.2 -
Gr	2.6	1 0.4 -	1 9.1 -			4 2.9	16 12.2 ++ N>S
Sa	4.9	1 0.4 -		1 2.7		3 2.2	18 13.8 ++ N>S
		L. toae	*L. tretocephalus*	*L. elongatus*	*L. fasciatus*	*L. lemairei*	*L. profundicola*
Ko	51.9	4 12.1 ++ N<S	25 29.6 ++ N<S	45 54.9		8 25.2 ++ N<S	13 81.1
St	15.9	14 43.9 ++ N>S	14 16.8 -	10 12.1	1 100.0	15 46.7 ++ N<S	1 5.7
Ru	24.7	12 37.4 -	35 41.8 ++ N>S	18 22.0		8 25.2 -	2 13.2
Gr	2.6	2 6.5 -	3 3.6 -	3 3.7		1 2.8 -	
Sa	4.9		7 8.2 -	6 7.3			
		J. marlieri	*J. transcriptus*	*T. caninus*	*T. temporalis*		
Ko	51.9	53 58.2	27 50.9	6 75.0	579 40.7 ++ N<S		
St	15.9	16 17.6	17 30.2	1 12.5	271 19.1 ++ N>S		
Ru	24.7	17 18.7	9 17.0	1 12.5	487 34.3 ++ N>S		
Gr	2.6		1 1.9		24 1.7 + N>S		
Sa	4.9	5 5.5			60 4.2		
		L. brichardi	*T. bifrenatus*	*A. leptura*	*E. cyanostictus*	*H. pfefferi*	*Ophthalmochromis* spp.
Ko	57.8	4,832 40.3 ++ N<S	977 69.0 ++ N>S	102 85.0 ++ N>S	57 82.6 ++ N>S	3 75.0	24 66.7
St	11.0	1,373 11.4 + N>S	167 11.8 -	5 4.2 + N<S	2 2.9 -		4 11.1
Ru	24.8	4,926 41.0 ++ N>S	168 11.9 ++ N<S	13 10.8 ++ N<S	9 13.0 + N<S		7 19.4
Gr	2.0	260 2.1 + N>S	7 0.5 ++ N<S		1 1.5 -		1 2.8
Sa	4.5	613 6.3 + N>S	96 6.8 ++ N>S			1 25.0	
		S. curvifrons	*S. diagramma*	*S. marginatus*	*T. irsacae*	*T. moorei*	*P. famula*
Ko	57.8	29 85.3 ++ N>S	25 89.3 ++ N>S	9 64.3	19 76.0	320 65.2 ++ N>S	6 60.0
St	11.0	5 14.7 -	2 7.1 -	1 7.1	3 12.0	61 12.1 -	1 10.0
Ru	24.8		1 3.6 -	2 14.3	3 12.0	101 20.1 + N<S	3 30.0
Gr	2.0					10 2.0 -	
Sa	4.5			2 14.3		3 0.6 ++ N<S	
		P. fasciolatus	*P. orthognathus*	*P. polyodon*	*P. trewavasae*	*L. dardennei*	*L. labiatus*
Ko	57.8		10 41.7	160 77.7 ++ N>S	50 61.0	17 65.4	27 69.2
St	11.0		6 25.0	13 6.3 + N<S	7 8.5	3 11.5	5 12.8
Ru	24.8	2 66.7	6 25.0	29 14.1 ++ N<S	23 28.0	6 23.1	7 17.9
Gr	2.0	1 33.3	1 4.2	4 1.9 -	1 1.2		
Sa	4.5		1 4.2		1 1.2		
		Xenotilapia sp.	*P. microlepis*	*P. straeleni*			
Ko	57.4	3 25.0 + N<S	118 64.1	4 50.0			
St	11.0	1 8.3 -	17 9.2	4 50.0			
Ru	24.8		34 18.5				
Gr	2.0		2 1.1				
Sa	4.5	8 66.7 ++ N>S	13 7.1				

Appendix 3. Mean concentration of every species and degree of spatial correlation. The numeral underlined shows $\hat{c}$ of each species and other is the value of ω.

spp. preferring rock

	S. curvifrons	S. diagramma	E. cyanostictus	A. leptura	P. polyodon	T. moorei	L. furcifer	L. elongatus	L. compressiceps	L. leleupi	P. microlepis	J. marlieri	J. transcriptus	L. dardennei	P. trewavasae	L. labiatus	Ophthalmochromis spp.
S. curvifrons	1.8	0.0	0.2	-1.0	0.2	0.2	-1.0	-1.0	-1.0	-0.6	-1.0	-1.0	-1.0	0.1	-0.4	0.1	0.1
S. diagramma		1.5	0.3	-0.5	0.3	0.3	0.0	-1.0	-1.0	-1.0	-0.3	-1.0	-1.0	0.0	-0.1	-1.0	0.1
E. cyanostictus			1.6	0.0	0.2	0.2	-0.3	-0.6	-1.0	-1.0	-0.4	-1.0	-1.0	0.0	0.0	-1.0	0.0
A. leptura				4.4	-0.9	-0.8	0.1	-0.6	-1.0	-0.8	0.0	0.1	0.1	0.1	-0.7	-0.4	-0.3
P. polyodon					1.7	0.5	0.0	-0.7	-0.7	0.0	-0.3	-0.8	-0.3	-0.3	-0.1	0.0	0.1
T. moorei						1.8	0.0	-0.7	-1.0	-0.1	-0.4	-0.7	-0.4	0.1	0.1	0.1	0.1
L. furcifer							1.6	-1.0	0.1	0.1	-0.2	0.2	0.4	-1.0	-0.3	-1.0	0.1

spp. preferring other substrate type

	T. bifrenatus	L. modestus	L. savoryi	L. brichardi	L. lemairei	L. tretocephalus	T. temporalis	L. elongatus	L. compressiceps	L. leleupi	P. microlepis	J. marlieri	J. transcriptus	L. dardennei	P. trewavasae	L. labiatus	Ophthalmochromis spp.
T. temporalis							2.6	0.0	-0.3	-0.1	0.1	-0.1	-0.3	0.0	0.0	-0.3	0.0
L. tretocephalus						1.2	-0.5	-1.0	0.0	0.0	0.0	-0.1	-0.2	-1.0	-0.4	-1.0	0.0
L. lemairei					1.5	-1.0	0.0	-1.0	-1.0	-1.0	0.0	-1.0	0.1	0.1	-1.0	-1.0	-1.0
L. brichardi				26.7	0.0	0.1	0.0	0.1	0.0	0.0	0.1	0.1	0.1	-0.1	-0.4	-0.4	-0.6
L. savoryi			4.0	0.2	0.2	0.1	-0.4	-0.9	-1.0	0.0	-0.6	-0.1	0.0	0.0	0.0	0.0	-0.6
L. modestus		1.3	-0.8	0.1	-0.3	-0.3	0.1	0.0	0.0	-0.2	-0.2	0.0	-1.0	-0.3	0.0	0.1	-0.8
T. bifrenatus	9.3	0.0	0.0	0.0	0.2	0.1	-0.1	0.0	0.0	0.0	0.1	0.3	0.2	-0.1	-0.4	-0.3	-0.3

ubiquitous spp.

	L. elongatus	L. compressiceps	L. leleupi	P. microlepis	J. marlieri	J. transcriptus	L. dardennei	P. trewavasae	L. labiatus	Ophthalmochromis spp.
Ophthalmochromis spp.	-0.4	-1.0	-0.2	-0.6	-0.8	0.0	-1.0	-0.2	-0.2	1.3
L. labiatus	-0.3	0.0	0.0	-0.6	-0.4	-1.0	0.7	0.0	1.1	
P. trewavasae	-1.0	0.1	0.0	0.0	-0.1	-1.0	-1.0	1.0		
L. dardennei	-1.0	-1.0	0.0	-0.6	-0.3	-1.0	1.2			
J. transcriptus	-0.5	-1.0	0.1	0.1	0.2	1.4				
J. marlieri	0.1	0.0	0.0	0.0	1.3					
P. microlepis	-0.4	-1.0	-0.2	1.5						
L. leleupi	-0.5	0.0	1.2							
L. compressiceps	0.0	1.2								
L. elongatus	1.4									