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FISH BIOMASS AND DENSITY IN MACROPHYTE HABITATS IN FLOODPLAIN LAKES OF THE ORINOCO BASIN, VENEZUELA

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ABSTRACT

The fish communities, in seven macrophyte biotopes, in the Orinoco drainage, were studied. The density and biomass of the fishes were estimated in three consecutive months, in the last part of the dry season. The estimates were derived from a dataset comprehending 177 samples. Sampling was carried out with a net, easily constructed from cheap and locally available materials. In total 25,239 fishes of 96 species and 33 families, varying in size from 20-418 mm in standard length. Fish density ranged from 43,000 to $1.55x10^6$ ind./ha, and it decreased during the study period, mainly due to depletion of the smallest fish (<50 mm). The biomass ranged from 293 to 2,530 kg/ha, these figures are among the highest reported from the tropics. The precision of the density and biomass estimates was evaluated using the index D (percentage standard error of the mean). In addition, the number of replicas necessary to obtain an error of 20 and 50 % were determined.

BIOMASA Y DENSIDAD DE PECES ASOCIADOS A MACROFITAS DE LAGUNAS INUNDABLES, CUENCA DEL ORINOCO, VENEZUELA

Palabras clave: Peces dulceacuícolas. Biomasa. Densidad. Macrofitas. Lagunas inundables.Orinoco.Venezuela.

RESUMEN

Se estudiaron las comunidades de peces en siete microhábitats de macrofitas en la cuenca del río Orinoco, Venezuela. La densidad y biomasa íctica fue estimada durante tres meses consecutivos al final de la estación seca. Las estimaciones de densidad y biomasa proceden de una serie de 177 muestras. Los peces se colectaron con una red sencilla, construida con materiales económicos disponibles en la localidad de estudio. En total fueron colectados 25.239 peces distribuídos en 96 especies y 33 familias, con un tamaño entre 20 y 418 mm (longitud estandar). La densidad de peces varió de 43.000 a $1,55x10^{6}$ ind./ha. La densidad disminuyó durante el estudio debido principalmente a la desaparición de los peces más pequeños (<50 mm). Los valores de biomasa 293-2.530 kg/ha se sitúan entre los más elevados de los trópicos. La precisión de las estimaciones de densidad y biomasa, fue evaluada con el índice D (porcentaje de error estándar del promedio). Se determinó el número de muestras necesario para obtener un error menor del 20 y 50%.

INTRODUCTION

Neotropical floodplain lakes are characterized by annual or biannual changes in water level due to fluctuations in river discharge, precipitation and evaporation. High turbidity and the alterations in lake depth often implies that the most important primary producers are either floating macrophytes (*Eichhornia*, *Salvinia*, *Pistia*, etc.) or emergent grasses/sedges (*Paspalum*, *Eleocharis*, *Oxycarium*, etc.) (Junk and Howard-Williams, 1984; Castroviejo and López, 1985; Sánchez and Vásquez, 1986; Junk and Piedade, 1993).

Several studies have shown that macrophyte habitats house abundant invertebrate populations (Junk, 1973; Blanco-Belmonte, 1989). Numerous authors have also stressed the importance of these habitats as shelters and feeding areas to the fish communities (eg. Mago, 1970; Cordiviola de Yuan *et al.*, 1984; Welcomme, 1985; Galvis *et al.*, 1989).

In the high water season, fishes migrate onto the floodplain to feed. When the water retreats, most fishes leave the floodplain again. Some fishes, with special adaptations, survive in floodplain lakes as do juveniles of species which use the lakes as nursery areas (Welcomme, 1985). As the dry season advances, lake depth and area decrease, and most of the aquatic vegetation withers. Fishes are concentrated, and extremely high fish densities are common. In this period fishes are susceptible to all kinds of predators, because of the lack of hiding places (Lowe-McConnell, 1987).

There seems to be no doubt about that the few macrophytes, which remain through the dry season, constitute an important habitat for many fish species. It is, however, difficult to sample this habitat quantitatively with traditional techniques.

STUDY AREA

Precipitation in the Orinoco river drainage is concentrated within a rainy season (June-October), which, after a short period of transition, passes into a dry season (February-May) with hardly any precipitation at all. The river level is strongly influenced by this seasonal rainfall. The year can therefore be divided into a high and a low water period. The difference between the highest and lowest river level (reached respectively in August and March) averages 13 m at Ciudad Bolívar (Zinck, 1986). Along the main stream, the lower Orinoco forms a fringing floodplain, which covers about 7,000 km^2 and contains 2,294 permanent floodplain lakes (Hamilton and Lewis, 1990a). In addition, an internal delta covering 70,000 km^2 is found between two major tributaries, the Apure and Meta (Welcomme, 1985). Fish faunas were studied in both types of floodplains.

In Apure, three permanent lakes (La Ramera, Las Ventanas and Dividivi) were studied. The lakes are situated very close to each other, and are sometimes interconnected during the high water season. They are located in Hato el Frío within 7°45′N - 7°55′N and 68°50′W - 69°00′W, between the villages El Samán and Mantecal. For a detailed description of the area, see Ramia (1967, 1972), Mago (1970), Sarmiento (1983), Castroviejo and López (1985), Machado-Allison (1987) and Señaris and Lasso (1993).

La Ramera was the largest of the studied lakes (154 ha in the dry season, and 714 ha in the rainy). The lake is connected with the Apure river and Caño Guaritico part of the year. The studied part of La Ramera was shallow (max depth less than one metre) and extremely turbid. Floating vegetation was prevalent, with a dominance of *Eichhornia azurea*.

The other two Apure lakes were small (Dividivi = 0.5 and Las Ventanas = 0.7 ha), and we named them after adjacent farms. These lakes are not directly connected with the river, and the construction of roads in the area means that these lakes are isolated for longer periods of time. Both lakes were more transparent than La Ramera, their maximum depths were less than one metre, and they possessed extensive belts of a sedge species preliminarily determined as *Scleria* sp.

In the fringing floodplain of the Lower Orinoco River two permanent lakes (Merecure and Castillos) close to Ciudad Guayana were chosen. The area is characterized by forested high plains separated from the river by levees. Floodplain lakes in this area are generally connected to the river with short canals through the levees, and are mainly filled by river water (Hamilton and Lewis, 1990a). The region around the Lower Orinoco was described by Sarmiento (1983), Colonnelo (1990a,b) and Hamilton and Lewis (1990a).

Merecure has an area of 78 ha at low water, and is situated about 60 km west of Ciudad Guayana (8°12′50′′N, 63°17′25′′W) (Hamilton and Lewis, 1990b). Maximum depth varies between 0.4 m in the last part of the isolation phase and 6 m at peak flood (Hamilton and Lewis, 1990b; pers. obs.). The aquatic vegetation was generally dominated by the grass *Paspalum repens*, but some macrophyte associations were dominated by the floating plants *Eichhornia crassipes* and *Salvinia* sp. *Paspalum repens* were generally encountered on deeper water than the floating plant species.

Castillos is located near "Los Castillos de Guayana" (8°30′2′′N, 62°21′15′′W - 62°23′45′′W) (Blanco-Belmonte, 1989). Maximum depth ranges from 0.7 m to 3.6 m depending on the season (Sánchez and Vásquez, 1986). The lake is not typical however, because the surface area varies very little between high and low water, 31.0 and 27.2 ha respectively (Vásquez, 1989). The vegetation in this lake was dominated by dense meadows of *Scleria* sp mixed with *E. crassipes* and *Salvinia* sp, during the sampling period.

MATERIAL AND METHODS

Sampling

Seven macrophyte biotopes were studied in three consecutive months of the dry season of 1992. The habitats were, according to the dominating macrophytes, classified as either "PASPALUM", "SCLERIA" or "FLOATING PLANT" (mainly *Eicchornia azurea*, *E. crassipes* and *Salvinia* sp.). Sampling was always carried out where one type of macrophyte clearly dominated (about 75% coverage). We made four to ten replicas in each habitat each month.

The sampling net was constructed of a plastic fly screen, with a mesh size of 1 mm. This material was cheap and proved to be strong and durable. When damaged repair was uncomplicated. The net measured 3.90 x 0.85 m, and was supplied with a 5 m rope along both the upper and lower rim. The lower part was in addition loaded with a chain weighted 1.9 kg along the entire length. The upper part was fitted with seven floats.

The net was easily handled, by two persons walking around in the shallow water, in the following manner: It was stretched out in front of a strip of dense vegetation, and pulled rapidly under the plants by the lower leaded end. When complete plant coverage was obtained, the leaded end was lifted free of the water, and the two ends brought together making up an oblong sack, which could be carried onto firm ground (Fig. 1). When beaches were not available, a boat was used.

All plants were carefully examined for small fishes and rinsed in a bucket of water, which was filtered again through the net. The fishes were preserved in formalin (10%) in a perforated plastic bag. To improve conservation, large specimens were opened with a short ventral cut, care being taken not to damage

Figure 1

The net was operated easily by two persons. It was pulled rapidly under the vegetation, lifted out of the water and brought onto firm ground, where the fishes were sorted out.

stomach and intestines. All fish species were identified and weighed in the laboratory with 0.1 g precision (formalin wet weight), and the standard length was measured to nearest millimeter. For knifefishes (Gymnotiformes) and swampeels (*Synbranchus marmoratus*) total length was measured.

Because of the patchy distribution of fish larvae, it was decided to exclude them from the study in order to minimise sample variance. This procedure, however, does not severely affect the density and biomass estimates, since the total number of larvae collected only constituted 2% of the total catch, and the number present in the individual samples usually did not exceed ten.

Sampling depth was determined by averaging three ruler measurements (nearest cm), along the edge of vegetation at the sampling stations. We assumed that the sampling system was so efficient that all fishes were caught from the area above each net haul. We determined biomass and density per unit of area by dividing the amount of fishes caught with the area of the net (3.3 m^2).

To evaluate the precision of the density and biomass estimates, the percentage standard error of the mean (D), and the number of replicas necessary to determine density and biomass with an accuracy of 20 and 50% were calculated (Elliot, 1971):

$$D = \frac{1}{\bar{X}}\sqrt{\frac{S^2}{n}} \quad \text{and} \quad n = \frac{S^2}{D^2\bar{X}^2}$$

Where D is the standard error of the mean, $\bar{X}$ is the mean S^2 is the sample variance and n is the number of replicas.

RESULTS

A total of 177 samples were taken, 88 "FLOATING PLANTS", 59 "SCLERIA" and 30 "PASPALUM". Ten plant species were recorded during the study (Table 1). The only important species outside the principal groupings was the submerged *Utricularia* sp.

Sampling depth ranged from 11 to 103 cm (Fig. 2). Samples in Dividivi, Las Ventanas and Castillos were, on the average, taken deeper than in La Ramera and Merecure. "PASPALUM" were sampled deeper than "FLOATING PLANTS" in Merecure.

In total, 25,239 fishes of 96 species, belonging to 33 families (Table 2), were caught during the study. Most of the fishes (83%) sampled during the study were < 50 mm (Table 3). Up to 98% of all fishes at a particular site and time were constituted by fish in this size group. Especially the macrophyte habitats in the lakes Castillos and Las Ventanas, were highly dominated by small fish, while their relative abundance were considerably less in La Ramera. In Merecure and Castillos, it was apparent that the relative abundance of small fish were higher in the grass biotopes ("PASPALUM" and "SCLERIA" respectively) than in the "FLOATING PLANT" biotope from the same lake. In all habitats there was a decrease in the relative abundance of small fish from the first to the last month.

Table 1
The plants registered in each lake during the study.

	Locality				
Taxa	**Ramera**	**Dividivi**	**Ventanas**	**Merecure**	**Castillos**
Salviniaceae					
Salvinia sp	*	*		*	*
Aracea					
Pistia sp	*				
Lemnaceae					
Lemna sp	*				
Pontederiaceae					
Eichhornia azurea Swartz					
E. crassipes Mart.	*	*	*	*	*
Marsiliaceae					
Marsilia sp					*
Onograceae					
Ludwigia sp	*	*			
Lentibulariaceae					
Utricularia sp	*	*	*		
Cyperaceae					
Scleria sp	*	*	*	*	*
Graminae					
Paspalum repens Berg				*	

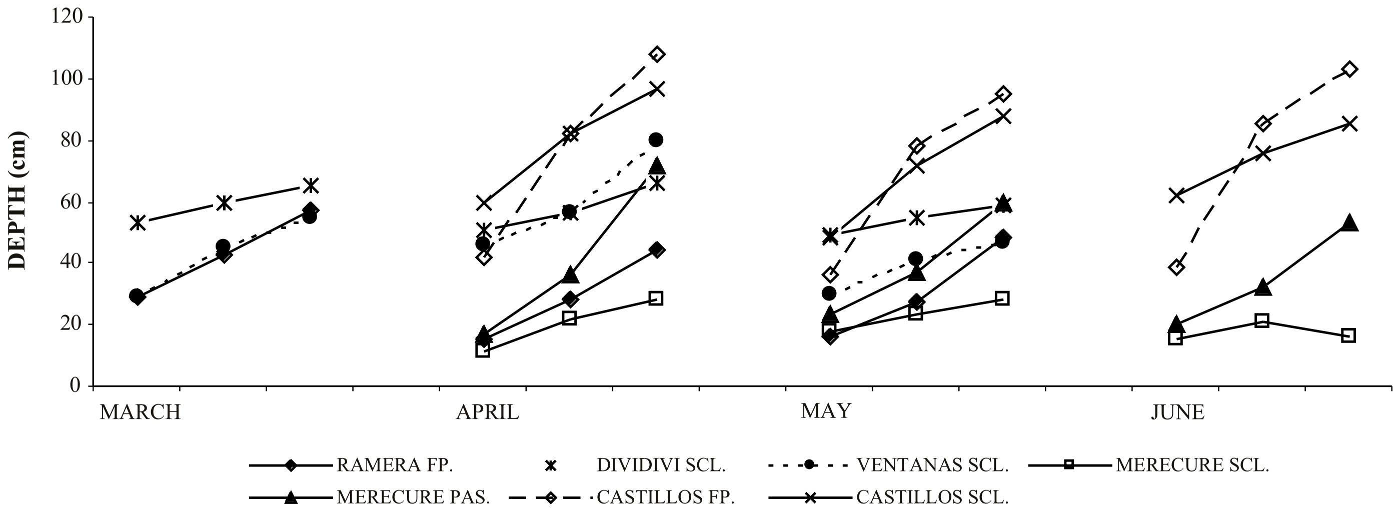

Figure 2
Minimal, maximal and mean sampling depth (cm) in each biotope and month during the study. FP.: "Floating plants", SCL.: "SCLERIA" and PAS.: "PASPALUM".

Almost all the fish families encountered were represented in the smallest size group, which consisted of a mixture of juvenile fish and adult miniature species. Most abundant, however, were characins (Characidae), clupeids, anchovies (Engraulidae) and trichomycterids. The larger size groups consisted mostly of knifefishes, cichlids, characins, and catfishes (Siluriformes). The largest fish caught was a *Sternopygus macrurus* measuring 418 mm; it was caught in the "FLOATING PLANT" biotope in Castillos.

Table 2
The fish families and orders sampled during the study.

CLUPEIFORMES (3)	**GYMNOTIFORMES (10)**
Clupeidae (1)	Apteronotidae (2)
Engraulidae (2)	Sternopygidae (5)
CHARACIFORMES (44)	Hypopomidae (2)
Characidae (24)	Gymnotidae (1)
Erythrinidae (2)	**SILURIFORMES (17)**
Ctenoluciidae (1)	Doradidae (4)
Cynodontidae (1)	Auchenipteridae (1)
Lebiasinidae (2)	Aspredinidae (1)
Characidiidae (1)	Pimelodidae (3)
Gasteropelecidae (1)	Trichomycteridae (2)
Prochilodontidae (1)	Callichthyidae (2)
Curimatidae (6)	Loricariidae (4)
Anostomidae (4)	**CYPRINODONTIFORMES (2)**
Hemiodontidae (1)	Poeciliidae (1)
PERCIFORMES (17)	Rivulidae (1)
Sciaenidae (1)	**SYNBRANCHIFORMES (1)**
Nandidae (1)	Synbranchidae (1)
Eleotridae (1)	**PLEURONECTIFORMES (1)**
Cichlidae (14)	Soleidae (1)
BELONIFORMES	
Belonidae (1)	

Density and biomass

According to the estimated densities and biomasses in the seven biotopes during the study period (Table 4), fishes were generally most abundant during the first of the three months and least during the last. The reduction in density was most dramatic in the two small lakes in Apure, with decreases of 80% and 85% in Las Ventanas and Dividivi, respectively. The highest density of 155.3 ind./m^2 among the studied biotopes was registered in Las Ventanas during March. The lowest density was recorded in Dividivi during May (just after the rains had begun) with 4.3 ind./m^2.

Biomass generally followed the same tendencies as density. The highest biomass was registered in Las Ventanas in March (253.0 g/m^2), the lowest in Merecure in the "FLOATING PLANT" biotope in April (29.2 g/m^2).

Table 3

The percentage relative abundance of each siza group of fishes in the monthly samples. FP.: "FLOATING PLANTS", SCL.: "SCLERIA" and PAS.: "PASPALUM". n: the number of replicas and N number of fish sampled.

	RAMERA FP.			VENTANAS SCL.			DIVIDIVI SCL.			MERECURE FP.			MERECURE PAS.								
SIZE GROUP	MARCH	APRIL	MAY	MARCH	APRIL	MAY	MARCH	APRIL	MAY	APRIL	MAY	JUNE	APRIL	MAY	JUNE	APRIL	MAY	JUNE	APRIL	MAY	JUNE
1- 50 mm	41	29	34	94	95	94	87	35	47	75	60	50	82	77	66	93	90	87	98	94	97
51-100 mm	26	35	33	6	4	3	12	58	47	12	15	21	5	4	8	4	5	4	1	3	1
101-150 mm	23	23	21	0	0	2	1	6	6	11	21	25	11	15	17	2	3	5	1	2	1
151-200 mm	5	10	10	0	0	0	0	1	0	2	3	2	2	3	4	0	0	1	0	0	0
201-250 mm	4	4	2	0	0	0	0	0	0	0	1	1	1	1	4	1	1	1	0	0	0
251-300 mm	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
301-350 mm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
351-400 mm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
401-450 mm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
n	9	10	10	5	5	5	4	5	5	10	10	10	10	10	10	10	10	9	10	10	10
N	861	1052	821	2574	804	529	389	83	72	687	630	490	1465	735	509	2340	2231	1024	2336	2909	2698

Precision of the method

The percentage error of the density estimates (D) ranged from 9-53% (Table 4). The error was less than or equal to 20% in 15 of 21 sampling situations. Two to 35 replicas were necessary to obtain an error of less than 20 %. The number needed to secure an error below 50% ranged from one to six.

Biomass estimates were less precise, D ranged from 14 to 54%. D was under or equal to 20% in nine situations. From four to 38 replicas were necessary to maintain an error beneath 20%, while one to nine replicas would have assured an error below 50%.

DISCUSSION

In tropical floodplain rivers, fishes are dispersed in the entire floodplain to feed during the high water season. When the water withdraws, fishes migrate to the main river or stay back in floodplain lakes until the next inundation. Fish abundance in lakes and pools usually decrease in the last part of the dry season. When the water evaporates, lakes become shallow, and the macrophytes wither, rendering fishes susceptible to predation. Mortality is high and most fish species do not reproduce until the beginning of the rains (Lowe-McConnell, 1987; Winemiller, 1989). The highest fish densities, however, are also seen during the early dry season. This is a consequence of the concentration of fishes in a decreasing volume of water (Mago, 1970; Taphorn and Lilyestrom, 1984; Machado-Allison and Royero, 1986; Lasso, 1996). The concentration effect might be reinforced in the macrophyte habitats, because the plants are decimated, resulting in further concentration of larvae and juveniles, which depend on their shelter.

Our results show very high densities and biomasses especially in the first month of the study (maximum 1.55 mill. ind./ha and 2,530 kg/ha). These figures are among the highest registered in tropical areas when compared with the compilations by Welcomme (1985) and Machado-Allison (1987), we must stress however that our figures only concern the vegetated areas and cannot be extrapolated to entire lakes. It must further be underlined that only the rim of the vegetation belt was sampled. Deeper inside the floating meadows oxygen levels may be so low that there possibly are no fish except swampeels, which can make use of oxygen from the atmosphere (Junk, 1973).

Our study concentrated on the last part of the dry season. We found that the density of fish generally decreased during the studied period. By the end of the dry season, the water became so shallow that the exchange of water, under the plants, was heavily reduced. In this situation elevated temperatures and deoxygenation under the macrophytes can be expected (Junk, 1973), probably forcing most fish out in the dangerous open water, at least during part of the day. The disproportionately high reduction in the number of the smallest fish was probably due to smaller fish being more vulnerable to predators than large ones.

Table 4

Density (above) and biomass (below) estimates in each biotope and month during the study. FP.: "FLOATING PLANTS", SCL.: "SCLERIA" and PAS.: "PASPALUM'. n: the humber of replicas, D: percentage standard error of the mean, n20 and n50: the number of replicas needed to maintain an error of 20 and 50% respectively.

	MARCH					APRIL					MAY					JUNE				
	DENSITY	D	n	n20	n50	DENSITY	D	n	n20	n50	DENSITY	D	n	n20	n50	DENSITY	D	n	n20	n50
RAMERA FP.	28.9	10	9	3	1	31.7	12	10	4	1	24.8	9	10	2	1	*	*	*	*	*
VENTANAS SCL.	155.3	16	5	4	1	48.5	18	5	4	1	31.9	53	5	35	6	*	*	*	*	*
DIVIDIVI SCL.	29.3	36	4	13	3	5.0	11	5	2	1	4.3	31	5	12	2	*	*	*	*	*
MERECURE FP.	*	*	*	*	*	20.6	27	10	19	3	19.0	18	10	8	2	14.8	13	10	5	1
MERECURE PAS.	*	*	*	*	*	44.2	18	10	9	2	22.2	10	10	3	1	15.4	14	10	5	1
CASTILLOS FP.	*	*	*	*	*	70.7	34	10	30	5	67.6	20	10	10	2	34.3	25	9	14	3
CASTILLOS SCL.	*	*	*	*	*	70.5	14	10	5	1	87.8	18	10	8	2	81.4	20	10	10	2

	MARCH					APRIL					MAY					JUNE				
	BIOMASS	D	n	n20	n50	BIOMASS	D	n	n20	n50	BIOMASS	D	n	n20	n50	BIOMASS	D	n	n20	n50
RAMERA FP.	177.9	19	9	9	2	157.9	15	10	6	1	121.1	25	10	17	3	*	*	*	*	*
VENTANAS SCL.	253.0	25	5	9	2	83.6	20	5	6	1	80.8	54	5	36	6	*	*	*	*	*
DIVIDIVI SCL.	123.7	18	4	4	1	94.4	19	5	5	1	47.7	32	5	14	3	*	*	*	*	*
MERECURE FP.	*	*	*	*	*	29.3	24	10	15	3	30.8	26	10	17	3	35.6	45	10	51	9
MERECURE PAS.	*	*	*	*	*	57.4	20	10	11	2	33.0	29	10	21	4	43.0	19	10	10	2
CASTILLOS FP.	*	*	*	*	*	73.2	21	10	11	2	89.0	14	10	5	1	55.8	30	9	20	4
CASTILLOS SCL.	*	*	*	*	*	33.5	38	10	36	6	73.6	27	10	19	3	56.1	16	10	7	2

The differences, in fish densities and relative abundance of different size groups, between the biotopes, are more difficult to explain with the current dataset. Plausible explanations include variation in predator densities, oxygen levels, transparency, and food availability. Piscivorous birds, for instance, were far more common on the shores of the three Apure lakes than around Merecure and Castillos.

Quantitative studies of fish in macrophyte habitats are sparse because of the difficulties involved with the sampling. Winemiller (pers. comm.) used a method similar to ours in vegetated areas of Caño Maracá, in the Venezuelan llanos. His density and biomass estimates ranged from 3.5 ind./m^2 and 7.9 g/m^2 (rainy season) to 27.6 ind./m^2 and 140.7 g/m^2 (transition period). In April 1988 (dry season) he found a density of 6.8 ind./m^2 and a biomass of 46.8 g/m^2. The figures for transition period and dry season are within the range of our results. Henderson and Hamilton (1995) studying an Upper Amazonian lake, Lago Mamirauá, found fish biomasses of 31.2 g/m^2 and 19.2 g/m^2 and corresponding densities of 9.0 ind./m^2 and 1.3 ind./m^2 in anchored and drifting vegetation respectively, during the period where the water was raising. Biomass and density figures, for anchored vegetation, are within the range of our results, while the density in drifting vegetation is lower than our minimum of 4.3 ind./m^2.

Catches in earlier published studies seem to be restricted to either small or large specimens. Geisler (cited by Junk, 1973) for example surrounded a 25 m^2 floating island of *Paspalum repens* completely with a net in the Amazonian várzea. He caught 1128 fishes (45 ind./m^2), but his sample can not be considered quantitative because of the large meshsize he used. Another attempt was done by Cordiviola de Yuan *et al.* (1984), in a floodplain lake of the Paraná River. Their densities ranged from 3 to 232 ind./m^2. These authors sampled with a dipnet with an area of 0.25 m^2 and with 1.5 mm meshsize. The advantage by using such a small sampler is that many replicas can be made. The disadvantage is the selectivity towards small fishes. Almost all specimens in their study were less than 5 cm.

Our study was carried out with a net, which, in addition to being cheap, strong and easily constructed, had a mesh size and a dimension that enabled us to catch a large array of fish species and sizes. We performed an intermediate number of replicas, and we were able to catch specimens from 2 to 42 cm, weighing from 0.1 g to 680.1 g. Our method nevertheless involved problems with some of the largest specimens of *Prochilodus mariae*, *Hoplias malabaricus* and *Cichla orinocensis,* because they were able to jump out of the net on some occasions. This of course primarily affects the biomass estimates, while the density estimates are almost unaffected, because of the low abundance of these species. Slight modifications of the net might prevent these individuals from escaping. Some fish may also have evaded the net by swimming under it when fishing in deep water. We consider this bias to be small, however, because samples were usually taken in water shallower than the depth of the net, and because most species in the studied habitats tend to hide themselves in the vegetation when disturbed (Pérez, 1984; Sazima and Zamprogno, 1985). Modifications may nevertheless be necessary for working under high water conditions.

Elliot (1971) suggested a precision of 20% as adequate, when considering samples of benthic invertebrates. Fishes, however, are much more mobile organisms, with higher chance of escaping, and more variation is to be expected. Calculations, of the number of samples necessary to obtain a 20% error, nevertheless show that the number of replicas taken (between four and ten) often was adequate. In some extreme situations however, 30-36 replicas would be necessary. If, on the other hand, a 50% error could be tolerated one to five replicas would generally have been sufficient. Biomass estimates were generally less precise than density figures, due to large specimens with low abundance, which augmented the variance of the weight. We believe that these levels of error are acceptable, and since there does not seem to be any direct relationship between precision of the two estimates and lake size, or the kind of macrophyte, this method could probably be applied in other macrophyte habitats too. For a precise determination of density and biomass of individual species, especially those of low abundance, more replicas would be needed however.

Our experience was that the effort needed for two persons to take ten samples is approximately five hours. One way of reducing the effort (with about 50%) could have been to omit the time consuming washing procedure. This would not have affected the results greatly, except where large amounts of swampeels or very small fishes were mixed with large amounts of organic material.

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