The fish fauna of Brokopondo Reservoir, Suriname, during 40 years of impoundment

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We investigated long-term changes in the fish fauna of Brokopondo Reservoir, Suriname, the first large reservoir (1560 km²) that was created in tropical rainforest. Before closure of the dam in 1964, the fish fauna of Suriname River had 172 species, high diversity and high evenness. The riverine fauna was dominated by small-sized species, but no single species was dominant in numbers. Large catfishes were dominant in biomass. Species were evenly distributed over riverine habitats: rapids, tributaries and main channel. Four years after closure of the dam, only 62 fish species were collected from Brokopondo Reservoir, but the composition of the fish fauna was still changing. The reservoir fauna in 1978 was very similar to the reservoir fauna in 2005, indicating that a stable equilibrium had been reached 14 years after closure of the dam. The reservoir fauna had 41 species, low diversity and low evenness. Most species of Suriname River and its tributaries with strict habitat requirements did not survive in Brokopondo Reservoir. Fish community structure was different among four habitats of Brokopondo Reservoir. The open-water habitat (10 species) was dominated by the piscivores *Serrasalmus rhombeus*, *Acestrorhynchus microlepis* and *Cichla ocellaris* and their prey *Bryconops melanurus* and two *Hemiodus* species. *B. melanurus* fed on zooplankton, Culicinae pupae and terrestrial invertebrates. *Hemiodus* fed on fine flocculent detritus, demonstrating that the detritus-based food chain was still important in late stages of reservoir development. *Serrasalmus rhombeus* also fed on peccaries that drowned when swimming across the large reservoir in rough weather. The shore community (27 species) was dominated by seven cichlids, but early stages and juveniles of the open-water species *S. rhombeus* and *B. melanurus* also occurred in the shore habitat. Fish biomass in the shore habitat was 66.5±59.9 kg ha⁻¹. The cichlid *Geophagus surinamensis* and the characid *B. melanurus* had a lower biomass in Brokopondo Reservoir than in Suriname River. *Serrasalmus rhombeus* showed reduced body length in Brokopondo Reservoir as compared to riverine populations.

Foram pesquisadas as modificações a longo prazo na ictiofauna do reservatório de Brokopondo, o primeiro de grande porte (1560 km²) construído em floresta tropical úmida. Antes do fechamento da barragem em 1964, a ictiofauna do rio Suriname possuía 172 espécies, com diversidade e equitabilidade altas. A fauna do rio era dominada por espécies de pequeno porte, mas nenhuma delas dominava em número de indivíduos. Em termos de biomassa, os grandes bagres eram dominantes. As espécies estavam homogeneamente distribuídas nos diferentes hábitats: corredeiras, afluentes e canal principal. Quatro anos depois do fechamento da barragem, somente 62 espécies de peixes foram coletadas no reservatório de Brokopondo, mas a composição da ictiofauna ainda estava mudando. Em 1978, a ictiofauna do reservatório era semelhante à de 2005, indicando que um equilíbrio estável foi atingindo 14 anos depois do fechamento da barragem. A ictiofauna do reservatório tinha 41 espécies, diversidade e equitabilidade baixas. A maioria das espécies do rio Suriname que tinham exigências estreitas de hábitat não sobreviveram no reservatório. A estrutura das comunidades de peixes foi diferente nos quatro hábitats do reservatório de Brokopondo. O hábitat das águas abertas (10 espécies) foi dominado pelos piscívoros *Serrasalmus rhombeus*, *Acestrorhynchus microlepis* e *Cichla ocellaris* e suas presas *Bryconops melanurus* e duas espécies de *Hemiodus*. *Bryconops* alimentou se de zooplâncton, pupas de Culicidae e invertebrados terrestres. *Hemiodus* alimentou se de detritos floculentos, demostrando que a cadeia alimentar baseada em detritos ainda era importante em estágios avançados de desenvolvimento dos reservatórios. *Serrasalmus rhombeus* também come queixadas que se afogam quando tentam atravessar nadando o grande reservatório em condições de mau tempo. A comunidade das margens (27 espécies) foi dominada por sete Cichlidae, embora estágios iniciais e juvenis das espécies de águas abertas (*i.e. S. rhombeus* e *B. melanurus*) também estivessem presentes nos hábitats da margem. A biomassa de peixes nos hábitats da margem foi de 66.5±59.9 kg ha⁻¹. O Cichlidae *Geophagus surinamensis* e o Characidae *B. melanurus* tiveram peso úmido menor no reservatório de Brokopondo do que no rio Suriname. *Serrasalmus rhombeus* apresentou comprimento menor no reservatório quando comparado com as populações do rio.

Key words: Dam, Man-made lake, Neotropical, River, Fish community.

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Introduction

Fishes of rivers and smaller streams are generally well adapted to deal with natural physical and chemical variations in space and time (Matthews, 1998), but when faced with human-induced alteration of their habitat most fishes die or escape from the disturbed stream. Habitat alteration is recognized as the single biggest cause of loss of freshwater fish diversity (Moyle & Leidy, 1992). The construction of a dam in a large river results in a profound and large-scale transformation of its ecosystem. Upstream of the dam, the lotic, cyclic and variable riverine environment changes into a reservoir with standing water, reduced water-level variability and reduced physical structure. Because freshwater fish represent a basic food resource for human populations in the tropics, fish communities and fisheries in tropical reservoirs have been intensively studied (*e.g.* Densen & Morris, 1999). Moreover, the high diversity of fish in tropical rivers allows in-deep ecological interpretations of the effects of damming on the functioning of fish communities (Mérona & Vigouroux, 2005). Reservoirs with their lake-like environmental conditions do not provide habitats for most riverine fishes and, following the construction of a dam, diverse tropical riverine fish communities were gradually replaced by simpler reservoir communities with reduced species richness and diversity (Lowe-McConnell, 1973; Vieira, 1982; Leite, 1993; Santos, 1995). Although studies of short-term changes in Neotropical fish faunas exist (*e.g.* Vieira, 1982; Leite, 1993; Santos, 1995; Ponton *et al.*, 2000; Mérona *et al.*, 2001, 2003; Mérona, 2002), few studies have addressed long-term impacts of dams on Neotropical fish communities (Agostinho *et al.*, 1999).

Brokopondo Reservoir (1560 km²) in the Suriname River, Suriname, is one of the oldest (dam closed 1 February 1964) large hydroelectric reservoirs (>1000 km²) in the tropics and the first large one in tropical rainforest (Goodland, 1979). Suriname River is a medium-sized (length 500 km, catchment 16,500 km², discharge 440 m³ s⁻¹ at outlet), clear-water (terminology of Sioli, 1950) river draining the weathered soils of the Precambrian Guayana Shield. Amazonian reservoirs pose particular problems related to intensive decomposition of inundated tropical rainforest vegetation (Tundisi *et al.*, 1993). Severe deterioration of water quality in the reservoir and downstream of the dam resulting in local (reservoir) to extensive (downstream) fish kills, explosive increase of free floating macrophytes, large-scale production of 'greenhouse' gases, and vertical stratification with an anoxic hypolimnion were first described for Brokopondo Reservoir (Donselaar, 1968; Heide, 1982; Panday-Verheuvel, 1983).

The Brokopondo Dam clearly had negative effects on the diverse Suriname River fish fauna (Boeseman, 1964; Mees, 1967; Nijssen, 1967, 1969), but impact assessment was hampered by poor taxonomic knowledge of Surinamese freshwater fishes at the time of dam construction. The large 1963-1964 collection of Suriname River fishes in the Brokopondo Reservoir Area by M. Boeseman was not studied in its entirety. Ouboter & Mol (1993) listed 86 fish species for the middle and upper Suriname River, but they did not examine the Boeseman collection. In 1967, Nijssen (1967, 1969; also

see Richter & Nijssen, 1980) collected only 62 fish species in Brokopondo Reservoir and in 1978 the number of reservoir fishes further declined to 37 species (Kapetsky, 1978; Richter & Nijssen, 1980). No surveys of Brokopondo Reservoir fishes have been carried out in the period 1978-2000 and it is not clear to what extent the reservoir fish communities had stabilized in 1978.

Agostinho *et al.* (1999) anticipated the following long term effects of reservoir aging on the fish fauna: a reduction in number of top-predators, mean size of species (and even within a species) and species richness, dominance of pelagic species and short-lived species with fast growth, and, in advanced stages of aging, dominance of species adapted to shallow water with low oxygen (first noticeable in littoral areas). Our objectives are to describe the pre-impoundment Suriname River fish fauna in the area of the future Brokopondo Reservoir (based on the 1963-1964 collection of Boeseman) and the fish fauna of Brokopondo Reservoir in 1967, 1978 and 2002-2005 in order to document impacts of the dam on the Suriname River fish fauna and long term changes in reservoir communities as hypothesized by Agostinho *et al.* (1999).

Material and Methods

Study site.

Suriname is situated between 2 and 6ºN on the northeast Atlantic coast of South America and has a humid tropical climate (Af according to the system of Köppen; Köppen, 1936). Rainfall averages 2270 mm/year in the Brokopondo Reservoir area. Brokopondo Reservoir (officially known as 'Prof. Dr. Ir. W.J. Van Blommesteinmeer') is situated at 4º45'N, 55º05'W in *terra firme* (high dry-land, *i.e.* not flooded in wet season) rainforest of the Precambrian Guayana Shield in the Suriname River Basin.

The Suriname River has a length of approximately 500 km, a catchment of 16,500 km², and a discharge of 440 m³ s⁻¹ at the outlet and 324 (214-756) m³ s⁻¹ at Afobaka (Amatali, 1993). Prior to closure of the dam, the Suriname River in the area of the future Brokopondo Reservoir was a low gradient (0.64 m per km) river with alternation of wide, shallow reaches with rapids and large river islands, and narrow, slowly flowing, deeper runs about 300 m in width and 5-7 m deep (Hydraulic Research Division, 1970; Heide, 1982). The rapids (up to 5 m high) probably presented no biogeographic barrier to dispersal of fishes as most species would have been able to bypass the rapids during the rainy season when water levels rise up to 5 m (Table 1). Drainage density was high and the river probably had narrow floodplains (approximately 10-200 m in width) without permanent lakes (similar to the middle Coppename River; Clarke & Rhodes, 2006). With 84.8% of its catchment in the weathered soils of the Guayana Shield, the Suriname River had many characteristics of a clear-water river (terminology of Sioli, 1950), *i.e.* low annual sediment transport (7000 m³/year at Brokopondo; Ringma, 1953), high Secchi-disc transparency (1-2 m), oligotrophic water (NO_3, NO_2, PO_4 and SO_4 <0.1 mg/L) with low conductivity (15-23 µS/cm), and pH 5.3-6.3 (Table 1). The water was saturated with dissolved

oxygen from surface to bottom, and water temperature varied between 27 and 31ºC (Table 1). Plankton was dominated by desmids and diatoms; zooplankton was sparse (Heide, 1982). Podostemaceae were abundant in rapids, and free floating macrophytes only occurred in small groups widely scattered along the banks (Donselaar, 1989). Shaded tributaries had higher conductivity, lower oxygen concentration, lower temperature, and less plankton than Suriname River.

The 54 m high dam at Afobaka, 194 river km from the estuary (Fig. 1), was constructed without fish ladders or other artificial devices to lessen the impact of the dam on fish migrations. The following description is based mainly on Heide (1982). The orientation of Brokopondo Reservoir is approximately north-south: the shortest distance from Afobaka Dam to Pokigron is 56 km and reservoir width averages 32 km (Fig. 1). The reservoir area at maximum normal water level is 1560 km^2; some 1160 hill tops (197 km^2) formed islands. Reservoir periphery shoreline is estimated at 1770 km, but total shoreline, including islands, is approximately 3700 km. The catchment of the reservoir is 12,550 km^2 (*i.e.* 76% of the Suriname River Basin). The reservoir was considered to be filled when the minimum water level for operation of the 180 MW power station, 41.2 m NSP ('Normaal Surinaams Peil' or New Surinamese Level), was reached in 1968. The water level had risen to the level of overflow in 1971. In 1971-1977, the average water level at Afobaka Dam (maximum depth of the reservoir) was 46.9 m NSP and corresponding mean depth 11.5 m. Within-year water level fluctuation varied between 1.4 and 5.3 m (Kapetsky, 1978). The volume of the reservoir is 22.7 km^3 at maximum water level of 48.2 m NSP and, given a yearly discharge of 9.7 km^3 year^{-1}, residence time of the water is approximately 28 months. The long residence time

reflects the small reservoir catchment and low relief in the reservoir area with average slope of the lake bottom 1.1%.

Chemical and biological developments in the forming reservoir were determined largely by (1) the change from turbulence and mixing under riverine conditions to stagnation and stratification in lacustrine conditions and (2) the decomposition of the drowned rainforest vegetation. Extreme consumption of dissolved oxygen by decaying forest litter and vegetation caused fish mortality, both in the reservoir and in the Suriname River downstream of the dam (Boeseman, 1964; Mees, 1967). In the period 1964-1967, a thermal stratification gradually developed in the reservoir following the death of trees (and loss of their leaves). In surface water (epilimnion), temperature, dissolved oxygen and transparency increased (Table 1) and a eutrophic plankton type with euglenas and zooplankton developed. Deep water (hypolimnion) remained anoxic with relatively low temperature, high electrolytes (conductivity) and gases H_2S and CH_4. The mineralization of organic matter of the inundated forest resulted in abundant growth of floating macrophytes, ultimately covering 582 km^2 (or 75% of the lake area) in 1966 (Donselaar, 1968). Aerial spraying with herbicide had eradicated most floating aquatic macrophytes by 1970, but decomposition of these water plants resulted in low dissolved oxygen levels in the hypolimnion in 1970-1976 (Panday-Verheuvel, 1983). The period 1980-2005 showed improvement in water quality and return to oligotrophy with >3 mg/L O_2 at the bottom of the lake (except at extreme depths), high dissolved oxygen >5.5 mg/L in surface water (0-5 m), conductivity 20-30 µS/cm, pH 5.5-7.0, and transparency of 3 m (Table 1). Shore vegetation of submerged or emergent macrophytes was poorly developed. Because

Table 1. Water quality of Suriname River and forest streams in future Brokopondo Reservoir area before closing of the dam in 1964 and Brokopondo Reservoir in the period 1964-present. Data are presented as minimum and maximum values, except for dissolved oxygen concentrations in Brokopondo Reservoir (means). Data sources are Van der Heide (1982)[1], Hydraulic Research Division (1970; years 1952-1964)[2], Hydraulic Research Division and Suralco Ltd aluminum company (unpublished)[7] and J. Mol and P. Ouboter (unpublished)[10]. In the period 1965-1967, water transparency increased in the reservoir[3], dissolved oxygen concentration increased in the epilimnion[5], and conductivity was low in surface water and high near the reservoir bottom as a result of decomposition of drowned forest vegetation and subsequent release of electrolytes[4]. The hypolimnion oxygen concentration decreased after spraying of water hyacinth with herbicide and subsequent decomposition of dead water plants on reservoir bottom[6]. In the months June-October 1985, hypolimnion water was anoxic[9]. The pH of deep hypolimnion water (20-25 m) was low (5.5-6.3 in 1981 and 4.3-5.2 in 1985) compared to surface water[8].

	Within-year water level variation (m)	Secchi-disk transparency (m)	Conductivity (0-5 m) (µS.cm^{-1})	pH (0-5 m)	Diss. oxygen (0-5 m) (mg.L^{-1})	Diss. oxygen (10-15 m) (mg.L^{-1})	Diss. oxygen (20-25 m) (mg.L^{-1})	Temperature (0-5 m) (ºC)	Temperature (20-25 m) (ºC)
Suriname River at Pokigron (km 273)[1]	2.8-4.5[2]	0.5-1.9	16-36	5.1-6.0	6.0-7.9			25.0-33.4	
Forest streams (tributaries to Suriname River)[1]	?	0.5-1.2	30-85	5.5-6.9	4.2-7.4			24.4-28.6	
Brokopondo Reservoir at Afobaka:									
1965-1967[1]	1.0-8.9	0.5-2.7[3]	30(-260)[4]	5.4-5.8	0.0-6.0[5]		0.0	27.5-34.5	25.0-26.0
1968-1969	3.1-5.7	2.0-3.4		5.5-6.3	4.5		3.2	28.0-32.0	26.5-28.5
1970	3.2	2.5-3.0		5.9-6.0	5.0		0.6[6]	28.5-31.5	26.5-28.5
1975	4.4	1.5-3.3	30-70	5.4-7.0	5.2		1.2	28.0-32.0	26.0-28.5
1981[7]		2.5-3.0	17-31	6.2-7.8[8]	6.4	3.3	1.4	29.3-31.2	27.9-28.5
1985[7]		2.5-4.0	23-44	5.0-5.7[8]	5.7	3.1	1.2[9]	28.0-31.3	27.4-29.0
2004[10]		1.6-3.0	27-33	6.7-7.3	7.0			29.1-33.1	

vegetation removal was not carried out and many hard-wood trees had a height of 20-30 m (Donselaar, 1989), approximately 70% of Brokopondo Reservoir still had tree trunks emerging from the water in 2005 (J.H. Mol pers. observation).
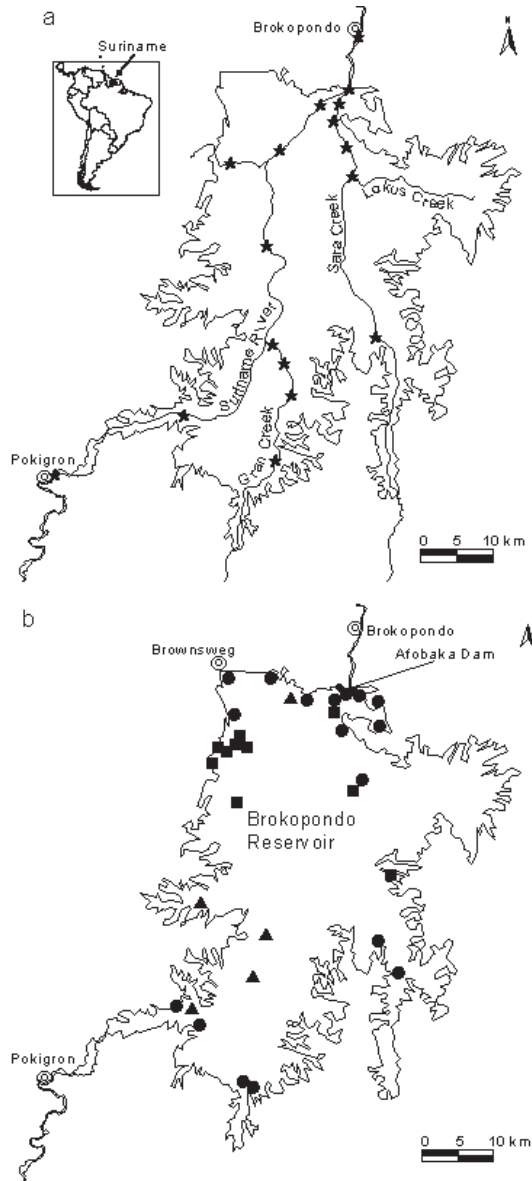

Fig. 1. Location and morphometry of Brokopondo Reservoir in Suriname showing fish sampling sites. (a) Former courses of the Suriname River and tributary streams in Brokopondo Reservoir area with pre-impoundment sampling sites (1963-1964; stars); outline of future Brokopondo Reservoir in grey. (b) Brokopondo Reservoir with sampling sites of fish surveys during filling stage (1965-1967; dots) and post-impoundment stage ([1978; triangles] and [2002-2005; squares]). The numerous small islands in the reservoir are not shown.

Some 5000 Maroons (descendants of escaped slaves) lived in the area inundated by the reservoir before its filling. These tribal people made a living from subsistence fishery, hunting and slash-and-burn agriculture. The maroons were relocated in new villages along the Suriname River above and below the reservoir (Leentvaar, 1973). The largest village in the area is Brownsweg (approximately 3000 inhabitants) at the north-west corner of the reservoir (Fig. 1). Other than small agricul-tural plots the only industries around the lake are logging and, since 1990, small-scale gold mining. No substantial fish-ery has developed on the reservoir during its 40-year exist-ence: fishing on a commercial scale is non-existent and sub-sistence and sport fishing are little developed (*e.g.* Kapetsky, 1978; Richter & Nijssen, 1980).

Fish surveys in the Brokopondo Reservoir area before and after closure of the dam

We analyzed fish collections from the pre-impoundment (1963-1964), filling (1966-1967) and post-impoundment (1978 and 2002-2005) phases of reservoir development.

In 1963-1964, Boeseman (1964) collected approximately 13,000 fishes of the Suriname River and its tributaries in the area of the future Brokopondo Reservoir. Boeseman used di-verse sampling devices such as seine, fish trap, cast net, hook-and-line and even explosives, but he collected most fishes with fish poison (Boeseman, 1964). Although Boeseman (1964) presented a tentative and incomplete list of fish genera of the Suriname River and certain taxa in his collection were studied in taxonomic revisions (*e.g.* Boeseman, 1968, 1971, 1982; Nijssen, 1970; Géry, 1972; Mees, 1974; Kullander & Nijssen, 1989), his large collection of Suriname River fishes was never studied in its entirety.

In the filling stage (1964-1967), the fish fauna of Brokopondo Reservoir was studied by Mees (1967) and Nijssen (1967, 1969).

In the post-impoundment stage, the fish fauna and fish-ery potential of Brokopondo Reservoir was studied in 1978 by Kapetsky (1978) and Richter & Nijssen (1980). Kapetsky (1978) published the results of one successful rotenone sample. Richter & Nijssen (1980) published the results of two gill net samples (open water habitat) and two rotenone samples (shore habitat). Our own collecting efforts in 2002-2005 were realized 40 years after closing of the dam and 34 years after the reservoir was filled.

Sampling procedures, fish identification and analyses

Eleven surveys of the fish fauna of Brokopondo Reservoir were conducted from April 2002 to February 2005. Fishes were collected in the eastern and northwestern part of the reservoir (Fig. 1). We distinguished four aquatic habitats: open water, sheltered bay, forested shore, and beach. The open water habi-tat still had numerous dead tree trunks emerging from the water surface, but wind action often resulted in turbulent water and large waves. Sheltered bays also had many dead tree trunks, but less wind and most of the time calm water. The forested shore habitat was found at the periphery of Brokopondo Res-ervoir where *terra firme* rainforest is bordered by a periodically flooded zone with dead bushes, woody debris and, locally,

clumps of submerged macrophytes in shallow water (up to 1.5 m in depth). Beaches of firm laterite rock substrate or sand were especially abundant in wave-exposed areas on islands where woody debris was washed away by wave action.

In the off-shore area (open water and sheltered bays), we collected fishes with 2 sets of 10 experimental gill nets (each gill net 25 m long and 2.5 m deep) with knot-to-knot mesh-sizes of 10, 15, 20, 25, 30, 35, 40, 50, 60 and 70 mm. The gill nets were attached to dead trees to prevent the nets from drifting away. Gill nets were set both during the night and during the day. A sample corresponded to 12 hours fishing with 1 set of 10 gill nets at a specific sampling station (*e.g.* one set of gill nets was placed in bay *x* for 12 hours [sample 1] and the next day this set of gill nets was moved to a different bay *y* for a second sample of bay fishes). It is known that gill nets are selective to fish, but the use of a large range of meshes of close dimension and the sampling in every hour of the day-night cycle reduce that bias. The beach habitat was sampled with 25-m long seine nets (2 and 10 mm knot-to-knot mesh). The shore habitat was sampled with 6.6% rotenone in concentration of approximately 0.25 g m^{-2} in five coves with an estimated surface area of 300, 300, 530, 600 and 1600 m^2 (maximum depth 1.5 m). The coves were blocked off with two block nets (length 25 m, depth 3 m, knot-to-knot mesh size 2 mm) attached 25 cm above the water surface to prevent jumping fish from escaping. Fishes were collected in the sampling area at 2 and 12 hours after poisoning.

Fishes were transported to base camp where they were identified, measured to the nearest millimeter standard length, and weighed to the nearest 0.1 g. Representative specimens were initially preserved in 4% formaldehyde, and then later transferred to 70% ethanol for long term storage at the National Zoological Collection of Suriname (NZCS) in Anton de Kom University of Suriname, Paramaribo. The stomach contents of fish species from the open water habitat were examined in the field (*Serrasalmus rhombeus* and *Cichla ocellaris*) or in the laboratory using a Wild M5-53340 stereo microscope. Stomach fullness was estimated as 0, 5, 25, 50, 75 or 100%. Stomachs with fullness ≥50% were retained for diet analysis. Food items were identified and grouped in eight categories: zooplankton (Cladocera, Ostracoda and Copepoda), Culicinae pupae, shrimps, fish, fine detritus, terrestrial invertebrates, terrestrial vertebrates and a rest group. The volume of food items was estimated as percentage of the total stomach contents and then adjusted for stomach fullness in all further calculations.

Fishes of the Suriname River prior to closure of the dam were studied in the 1963-1964 collection of M. Boeseman in Naturalis Museum (formerly Rijks Museum voor Natuurlijke Historie, RMNH), Leiden, the Netherlands. For each sample, we identified the species and then counted the number of specimens per species and measured total wet mass per species to the nearest 0.1 g and standard length to the nearest millimeter.

Fishes were identified with keys in general taxonomic treatises like Géry (1977) and Burgess (1989), regional contributions like Eigenmann (1912), Planquette *et al.* (1996), Keith *et al.* (2000) and Le Bail *et al.* (2000) and taxonomic surveys specific to Suriname like Nijssen (1970), Boeseman (1968, 1971, 1982), Kullander & Nijssen (1989), and many others. Maxi-mum standard length of species was obtained mainly from Reis *et al.* (2003). Categorization of habitat use of adults in riverine conditions was based on personal observations (JHM and PEO). Analysis of differences in community structure was based on relative abundance, the proportions in numbers and biomass of each species in the samples. Proportions (in biomass or numbers) of total sample belonging to *i*th species (p_i) were used to calculate species diversity with the Shannon-Wiener index (Krebs, 1989). Evenness (*J*) was also calculated according to Krebs (1989).

Statistical analysis

Because raw numbers or biomass cannot be compared among samples taken with different sampling methods, we converted fish numbers and biomass to proportions of the total sample (*i.e.* relative abundance of the species) to assess semi-quantitatively differences among habitats (*e.g.* shore and open water) and collection periods (*i.e.* Suriname River 1963-1964, Brokopondo Reservoir 1978 and Brokopondo Reservoir 2002-2005). Fish community structure was described by composition at species and family level (in number of specimens and biomass), number of species, species diversity (*H*), and equitability (*J*). Differences in fish community structure among reservoir habitats in 2002-2005 were assessed at the family level by ANOVA with arcsine-transformed proportions after testing for normality and homogeneity of variances. Differences in fish community structure between Suriname River (1963-1964) and Brokopondo Reservoir (2002-2005) and between Brokopondo Reservoir in 1978 and 2002-2005 were assessed with Wilcoxon's signed-ranks test using average proportions. Differences in relative biomass of fish species between Suriname River (1963-1964) and Brokopondo Reservoir (2002-2005) were assessed with Student's *t*-test after testing for normality. Significance was accepted when $p < 0.05$.

Results

The fish fauna of Suriname River before the closure of the dam

We counted 12842 fishes with a wet biomass of approximately 176.4 kg in 168 species in Boeseman's 1963-1964 collection of fishes of the Suriname River and its tributaries in the area of the future Brokopondo Reservoir (Appendix 1, Table 2). Species diversity (numbers/biomass) of the Suriname River fish fauna was high (4.11/3.76), as was evenness (0.80/0.74). In number of individuals and species, the riverine fauna was dominated by small-sized fishes (≤20 cm SL) (Table 3), but there was no singly dominant species. The cichlid *Geophagus surinamensis* was the most abundant species (5.7 %), but 15 other species also had a relative abundance of 2-5%. In biomass the fish fauna was dominated by large (≥30 cm SL) catfishes *Brachyplatystoma filamentosum* (17.0%; a single specimen of 170 cm TL with conservatively estimated wet mass of 30 kg), *Pseudoplatystoma fasciatum* (4.5%), *Pimelodus ornatus* (2.9%) and *Platydoras dentatus* (2.3%), and the medium-sized characoids *C. cyprinoides* (6.6 %), *H. unimaculatus* (4.5 %), *A. microlepis* (2.3%) and *Brycon falcatus* (2.0%) and cichlids *G. surinamensis* (4.9 %) and *C. saxatilis* (2.1%) (Appendix 1, Table 3). Species were relatively evenly distributed over habitat

categories, although surface fishes were somewhat under represented (Table 3). Habitat generalists were dominant in number of individuals and, to a lesser extent, in biomass. Large catfishes from the bottom of the main river channel were dominant in biomass. Four additional species, absent in the 1963-1964 collection of Boeseman, were caught in the Brokopondo Reservoir area before or after closure of the dam: *Plagioscion squamosissimus*, *Serrasalmus eigenmanni*, *Micropoecilia bifurca* and *Megalops atlanticus* (Appendix 1).

The fish fauna of Brokopondo Reservoir in 1967 and 1978

In 1967, four years after closure of the dam, Nijssen (1967, 1969) collected 62 fish species in Brokopondo Reservoir (Appendix 1, Table 2), but the reservoir fish fauna was clearly still in transition as shown by conspicuous fish species that were collected in 1967 but not in 1978 and 2002-2005, *e.g. Hoplerythrinus unitaeniatus*, two hatchet fishes (Gasteropelecidae), electric eel (*Electrophorus electricus*), the gymnotiform knifefish *Gymnotus carapo*, the cichlids *A. tetramerus*, *A. steindachneri* and *N. anomala*, and some medium to large-sized catfishes (*Callichthys callichthys*, *Megalechis thoracata*, *Trachelyopterus galeatus*, *Hemisorubim platyrhynchos*, *Pseudoplatystoma fasciatum* and *Batrachoglanis raninus*). In 1978, 35 fish species were recorded from Brokopondo Reservoir (Kapetsky, 1978; Richter & Nijssen, 1980; Appendix 1, Table 2); species diversity (numbers/biomass) was 1.82/2.04 and evenness was 0.75/0.61. The open water community had only 11 species, low species diversity 1.49/0.46 (numbers/biomass), and evenness 0.62/0.19. The shore community had 31 species, species diversity 1.48/2.26 (numbers/biomass), and evenness 0.60/0.65.

The fish fauna of Brokopondo Reservoir in 2002-2005

In 2002-2005, we collected 6474 fishes with a biomass of

Table 2. Fish community parameters for Suriname River (pre-impoundment 1963-1964) and four different habitats in Brokopondo Reservoir in 1966-1967, 1978 and 2002-2005. Biomass of shore fish community in 1978 is given in kg per ha[1].

		Number of specimens	Biomass (kg)	Number of species	Species diversity H (numbers / biomass)	Evenness J (numbers / biomass)
Suriname River 1963-1964		12842	176.4	172	4.11 / 3.76	0.80 / 0.74
Brokopondo Reservoir 1966-1967		-	-	62	-	-
Brokopondo Reservoir 1978	Open water	301	67.9	11	1.49 / 0.46	0.62 / 0.19
	Shore	2540	26.0[1]	31	1.48 / 2.26	0.60 / 0.65
	Total	2841	-	35	1.82 / 2.04	0.75 / 0.61
Brokopondo Reservoir 2002-2005	Open water	1511	110.9	10	0.88 / 0.62	0.38 / 0. 27
	Shore	2308	20.5	27	2.29 / 2.43	0.70 / 0.74
	Bay	2020	110.5	23	1.58 / 1.51	0.51 / 0.48
	Beach	636	5.2	11	1.31 / 1.81	0.54 / 0.75
	Total	6475	247.1	41	2.17 / 1.53	0.60 / 0.42

Table 3. Size (maximum Standard Length; cm) distribution of fish faunas of Suriname River Basin (1963-1964) and Brokopondo Reservoir (2002-2005), and habitat distribution of fishes of Suriname River Basin and representation of fishes from riverine habitats in Brokopondo Reservoir; proportions in number of specimens N, wet mass M, number of species (/ %) and richness (S). The habitat generalist category contains species well represented in more than one habitat (main channel, tributary, rapid)[1]. The tributary-leaf litter/debris category contains species from leaf litter and woody debris habitats[2].

	Suriname River (1963-1964)			Brokopondo Reservoir (2002-2005)		
	N %	M %	S (/ %)	N %	M %	S (/ %)
Size category (SL$_{max}$ in cm)						
1-10	43.41	10.35	69 (/40.1)	4.25	0.38	5 (/13.5)
11-20	29.14	21.87	46 (/26.7)	57.34	10.19	9 (/24.3)
21-30	14.97	26.72	26 (/15.1)	21.83	13.60	12 (/32.4)
31-40	8.65	11.96	13 (/ 7.6)	0.50	3.29	6 (/16.2)
41-50	2.70	4.46	5 (/ 2.9)	15.94	71.38	3 (/ 8.1)
51-60	0.24	0.87	3 (/ 1.7)	0.00	0.00	0
>60	0.81	24.19	8 (/ 4.6)	0.17	1.17	2 (/ 5.4)
unknown	0.17	0.01	2 (/ 1.2)	0.00	0.00	0
Habitat category						
Generalist[1]-surface	5.86	4.84	6 (/ 3.5)	38.12	7.84	3 (/ 8.1)
Generalist-column	42.98	27.19	22 (/12.8)	20.87	7.34	12 (/32.4)
Generalist-bottom	6.34	7.87	14 (/ 8.1)	21.59	6.87	6 (/16.2)
Main channel-surface	1.54	2.80	5 (/ 2.9)	0.23	0.23	2 (/ 5.4)
Main channel-column	4.09	9.25	16 (/ 9.3)	15.82	76.81	8 (/21.6)
Main channel-bottom	3.15	30.33	12 (/ 7.0)	0.05	0.83	2 (/ 5.4)
Tributary-surface	5.12	0.69	6 (/ 3.5)	0.00	0.00	0
Tributary-column	9.04	2.69	19 (/11.0)	3.08	0.04	2 (/ 5.4)
Tributary-bottom	7.53	4.57	12 (/ 7.0)	0.02	0.00	1 (/ 2.7)
Tributary-leaf litter/debris[2]	3.97	0.94	20 (/11.6)	0.00	0.00	0
Rapids-column	3.20	4.24	8 (/ 4.6)	0.00	0.00	0
Rapids-bottom	2.46	2.42	12 (/7.0)	0.00	0.00	0
migratory	0.32	0.48	4 (/ 2.3)	0.00	0.00	0
unknown	4.49	2.12	16 (/ 9.3)	0.25	0.05	1 (/ 2.7)

247.1 kg in 37 species in 54 samples in Brokopondo Reservoir (Appendix 1, Table 2). An asymptote in the species accumulation curve was reached in 2004, and four samples in February 2005 yielded no additional species. Species diversity was 2.17/1.53 (numbers/biomass) and evenness 0.60/0.42. In 2000, Mol *et al.* (2001) caught four additional species in Brokopondo Reservoir and thus we estimate that 41 fish species occurred in the reservoir (Appendix 1). We collected no exotic or invasive fish species in Brokopondo Reservoir; *i.e.* all reservoir species were also collected in Suriname River in 1963-1964 (Appendix 1).

At the family level (Appendix 1), fish community structure was significantly different among four habitats of Brokopondo Reservoir. Anostomids were found in higher relative abundance (ANOVA; $p < 0.001$) and relative biomass ($p < 0.05$) in sheltered bays than in shore habitat and they were not collected in open water and beach habitats. The open water and sheltered bay habitats had a higher relative abundance of Characidae than the shore habitat ($p < 0.05$). Hemiodontids were found in higher relative abundance ($p < 0.0001$) and biomass ($p < 0.01$) in open water than in beach, shore and bay habitats. Serrasalmids (mainly *Serrasalmus rhombeus*) were found in higher relative abundance ($p < 0.0001$) and biomass ($p < 0.00001$) in open water and sheltered bays than in shore and beach habitats. Cichlids were found in higher relative abundance ($p < 0.0001$) and biomass ($p < 0.0001$) in shore habitat than in beach habitat and in beach habitat they had a higher relative abundance and biomass than in open water and sheltered bays. Erythrinidae (*Hoplias malabaricus*), Doradidae (*Platydoras dentatus*), Loricariidae (*Hypostomus surinamensis* and *Loricariichthys maculatus*) and Sternopygidae (*Sternopygus macrurus*) were collected only in shore habitat.

We collected 1511 fishes with a total wet biomass of 110.9 kg in 17 samples in open water habitat (Appendix 1, Table 2). The fish community of open water had only 10 species (with 2 species, *Curimata cyprinoides* and *Myleus rubripinnis*, represented by a single specimen), low species diversity (0.88/0.62; numbers/biomass) and low evenness (0.38/0.27). The open-water fish community was dominated by the piscivores *S. rhombeus* (86.0% of fish biomass) and *Acestrorhynchus microlepis* (3.6%), and their main prey *Bryconops melanurus* (66.8% of specimens caught) and the two *Hemiodus* species (2.6% of numbers). *B. melanurus* fed near the surface on zooplankton, Culicinae pupae and terrestrial invertebrates (Table 4; Fig. 2). *Hemiodus* fed near the bottom on fine, flocculent detritus with uniform particle size, while *Cichla ocellaris* preyed on benthic shrimps (*Macrobrachium*). *Acestrorhynchus* preyed near the surface on *B. melanurus*. *S. rhombeus* showed opportunistic feeding behavior in preying on *Hemiodus argenteus* and *H. unimaculatus* near the bottom, *B. melanurus* near the surface and also showing cannibalism in eating juveniles (85-135 mm). When, in June 2002, a pack of white-lipped peccaries (*Tayassu pecari*) drowned while crossing the reservoir in rough weather, *S. rhombeus* also fed opportunistically on these peccaries.

The fish community of sheltered bays (2020 fishes, 110.5 kg; 25 samples) had 23 species, species diversity of 1.58/1.51 (numbers/biomass) and low evenness of 0.51/0.48 (Appendix 1, Table 2). The fish species that dominated the community in numbers or biomass were the same species that dominated the open water habitat fish community (*S. rhombeus*, *B. melanurus*, *A. microlepis* and the two *Hemiodus* species), but a number of other species were also well represented (*e.g. Leporinus fasciatus*, *Schizodon fasciatus*, *Chalceus macrolepidotus*, *Moenkhausia grandisquamis*, *Poptella brevispina*, *Roeboides thurni*, *Curimata cyprinoides*, *Prochilodus rubrotaeniatus*, *Myleus rubripinnis*, *C. ocellaris* and *Plagioscion squamosissimus*).

In five rotenone samples in shore habitat we collected 2308 fishes (20.5 kg) in 27 species (Appendix 1, Table 2). Both species diversity (2.29/2.43; numbers/biomass) and evenness (0.70/0.74) were high. Total fish biomass amounted to 66.5±59.9 kg ha^{-1} (mean±SD; range: 16.6-164.8 kg ha^{-1}). The shore community was dominated by *H. argenteus* and seven cichlids: *Geophagus surinamensis*, *Guianacara owroewefi*, *Cichlasoma bimaculatum*, *Krobia guianensis*, two *Crenicichla* species, and juvenile *C. ocellaris*. Other species well represented in the shore community were the anostomids *Leporinus friderici* and *L. fasciatus*, *B. melanurus*, *Hemigrammus boesemani* (in submerged macrophytes), *Bivibranchia simulata*, *C. macrolepidotus*, *H. malabaricus*, and the loricariid catfish *L. maculatus*. In clumps of submerged macrophytes, we collected early stages of *S. rhombeus* (30±4.29 mm, 1.0±0.31 g; n = 17). Small-sized *B. melanurus* (2 specimens of 37 and 39 mm SL; n = 144) were also collected in the shore habitat; in open water *B. melanurus* had SL > 60 mm (n = 1010).

We collected 636 fishes (5.3 kg; 7 samples) in 11 species in beach habitat (Appendix 1, Table 2). Species diversity was 1.31/1.81 (numbers/biomass) and evenness was 0.54/0.75. The beach community was dominated by *H. argenteus*, *B. melanurus*, *M. grandisquamis*, and the cichlids *C. ocellaris* (juveniles) and *G. surinamensis*.

Comparison of the fish faunas of Suriname River and Brokopondo Reservoir

At the family level (Appendix 1) fish community structure was significantly different among Suriname River (1963-1964) and Brokopondo Reservoir (2002-2005) both in relative abundance (Wilcoxon's signed-rank test; $p = 0.011$) and biomass ($p = 0.002$). The characoid families Anostomidae, Curimatidae and Gasteropelecidae decreased in relative abundance and biomass after damming, while Hemiodidae and Serrasalmidae (mainly *S. rhombeus*) increased in numbers and biomass. Brokopondo Reservoir had almost no Gymnotiformes (only *S. macrurus* was collected in the reservoir) and Siluriformes; all families in these orders were negatively affected by the dam. With the exception of two small species from leaf litter in tributaries (*Nannacara anomala* and *Apistogramma steindachneri*), cichlids were less affected by the change from riverine to reservoir conditions.

Of 172 species known to have occurred in the Suriname River in the reservoir area only 41 were collected in Brokopondo Reservoir in 2002-2005 (Appendix 1). When compared to the original Suriname River fish fauna, fish communities of Brokopondo Reservoir showed low species diversity and evenness (Table 2) with dominance of only a few species (Fig. 3). Brokopondo Reservoir had a low proportion
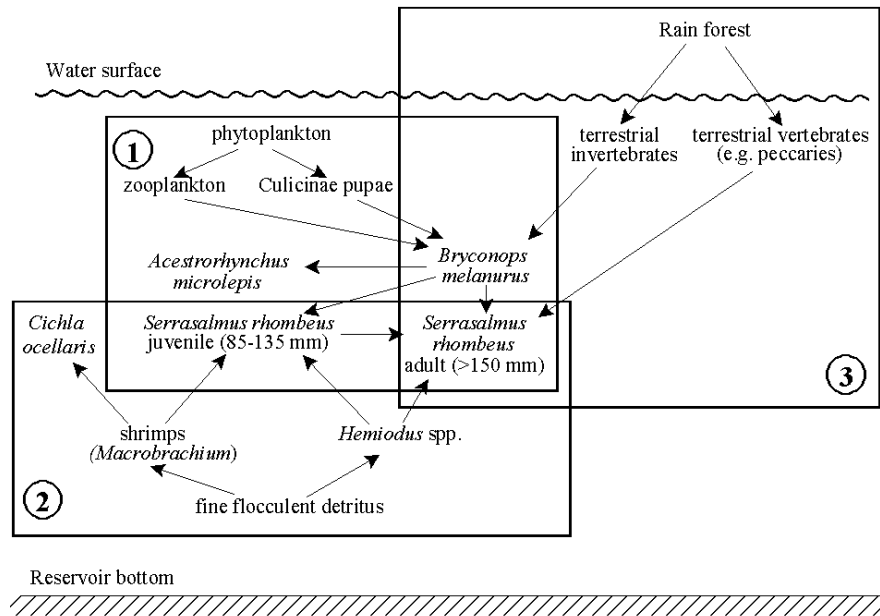
Fig. 2. Food web of the open-water habitat of Brokopondo Reservoir based on fish stomach content analysis. Food chains are based on autochthonous autotrophic production (1), fine, flocculent detritus of unknown origin (2) and, to a lesser extent, allochthonous production of the rain forest (3).

of small-sized species and individuals ($\leq$10 cm SL) and a low biomass of large-sized (> 60 cm SL) fishes compared to the Suriname River fish fauna (Table 3), but these differences in size-class distribution between riverine and reservoir faunas were not significant (Wilcoxon's signed ranks test; $p > 0.05$). *B. melanurus* (t-test, $p < 0.0001$) and *G. surinamensis* ($p < 0.01$) had a lower average wet mass in Brokopondo Reservoir than in Suriname River before closure of the dam (Table 5). Large piranhas *S. rhombeus* >300 mm were rare in Brokopondo Reservoir (0.8% of 762 specimens; SL_{max} 340 mm) as compared to the Suriname River before closure of the dam (6.8% of 74 specimens; SL_{max} 385 mm; Géry, 1972).

Habitat generalists (*e.g. B. melanurus*, *Hemiodus* spp, and cichlids) and midwater species from the main river channel (*e.g. S. rhombeus*) were well represented in the fish fauna of Brokopondo Reservoir. In 57 species from tributary forest creeks, including 20 small-sized species from leaf litter and woody debris, only 3 survived in the reservoir (Table 3). All

catfish and characoid species from riverine rapid habitat were lost from the area (Table 3).

Comparison of the fish faunas of Brokopondo Reservoir in 1978 and 2002-2005

The fish communities of Brokopondo Reservoir in 1978 and 2002-2005 were similar in number of species, species diversity and evenness (both the fish fauna of the reservoir in its entirety and the communities of open water and shore habitat). At the family level the structure of the fish communities of both open water (Wilcoxon's signed-rank test; p,numbers = 0.18; p,biomass = 0.84) and shore habitat (p,numbers = 0.69; p,biomass = 0.66) did not differ significantly between 1978 and 2002-2005 (Appendix 1). Both in 1978 and 2002-2005, the open water community was dominated by *B. melanurus* (numbers), *S. rhombeus* (numbers and biomass) and, to a lesser extent, *Hemiodus* (numbers only) (Fig. 3). Cichlids were dominant in number and biomass in the

Table 4. Diet of fishes from the open water habitat of Brokopondo Reservoir, 2002-2005. Data are average percentages by volume of each food item in stomachs with >50% fullness (n). The rest category contains mainly aquatic insects (1.99% in *B. melanurus*) and/or chitinous remains[1]. In 6 stomachs of *A. microlepis* the prey species was *Bryconops melanurus*; in other stomachs the prey species could not be identified[2]. Zooplankton in stomachs of *B. melanurus* consisted mainly of Ostracoda (17.60%) and Cladocera (7.03%) with only few Copepoda (0.11%)[3]. Detritus in *Hemiodus argenteus* and *H. unimaculatus* included 1.41% and 2.35% sand, respectively[4,5]. In one stomach of *Serrasalmus rhombeus* a crab (1.26%)[6] was present and in 6 stomachs the remains of white-lipped peccaries (*Tayassu pecari*) (*e.g.* hoofs, hair; 12.7%) were found[8]; fish prey species identified from *S. rhombeus* stomachs were *B. melanurus* (3 stomachs), *Hemiodus* spp. (3 stomachs), *Plagioscion squamosissimus* (1 stomach) and *S. rhombeus* (1 stomach)[7].

Species	n	zooplankton	Culicinae pupae	shrimps	fish	fine detritus	terrestrial invertebrates	terrestrial vertebrates	rest group[1]
Acestrorhynchus microlepis	11	0.57	0.00	0.00	96.00[2]	2.86	0.00	0.00	0.57
Bryconops melanurus	52	24.74[3]	48.36	4.42	2.21	0.66	15.40	0.00	3.98
Hemiodus argenteus	24	1.61	0.00	0.00	0.00	98.18[4]	0.00	0.00	0.21
Hemiodus unimaculatus	8	0.00	0.00	0.00	0.00	97.77[5]	0.35	0.00	1.88
Serrasalmus rhombeus	43	0.00	0.00	6.29[6]	77.04[7]	0.00	1.26	12.70[8]	2.70
Cichla ocellaris	4	0.00	0.00	100.00	0.00	0.00	0.00	0.00	0.00

more diverse shore community, but other species (miscellaneous group) were also abundant (Fig. 3). Fish biomass in the shore habitat was 17.4-31.5 kg ha^{-1} in 1978 (Kapetsky, 1978; Richter & Nijssen, 1980) and 16.6-164.8 kg ha^{-1} in 2002-2005 (or 16.6-69.4 kg ha^{-1} when excluding the outlier 164.8 kg ha^{-1}).

Discussion

When comparing our results with studies of other Amazonian reservoirs, differences in sampling methods and status of taxonomic knowledge of regional fish faunas should be considered. The impact of Amazonian reservoirs on riverine fish faunas was studied by comparing pre- and post-impoundment faunas based on (size-selective) gill net samples in the main river channel and reservoir (*e.g.* Vieira, 1982; Novoa *et al.*, 1991; Leite, 1993; Santos, 1995; Mérona *et al.*, 2003), thus probably undersampling small-sized species and species from specific riverine (tributaries, rapids and floodplain lakes) and reservoir (shore) habitats. In the present study, fishes were collected by diverse methods, including rotenone, gill nets, seine and other devices (*e.g.* Boeseman, 1964), and in diverse habitats. However, large catfishes of mid-channel bottom habitat were undersampled in the present study.

In 1967, four years after closure of the dam, the fish fauna of Brokopondo Reservoir was still changing. *S. rhombeus*, *B. melanurus* and *C. ocellaris* were already 'abundant' in the reservoir (Nijssen, 1967, 1969), but only 26 in 62 species of the reservoir fauna in 1967 were collected during the present study. In 1978, reservoir fish communities had apparently achieved stable equilibrium because (1) number of species, species diversity and evenness were very similar in 1978 and 2002-2005, (2) in open-water and shore habitat community structure at the family level did not differ between 1978 and 2002-2005, (3) in both 1978 and 2002-2005, the open water was dominated by piranha *S. rhombeus*, *B. melanurus*, *A. microlepis* and two *Hemiodus* species, while the more diverse shore community was dominated by seven cichlids, and (4) fish biomass in the shore habitat was of the same order of magnitude in 1978 and 2002-2005. Chemical and biological events associated with the filling of a new reservoir such as anoxia, eutrophication, plankton blooms and colonization by fishes vary with characteristics of the inundated terrestrial vegetation, basin morphology, and duration of the filling stage (Baxter, 1977; Agostinho *et al.*, 1999). Amazonian reservoirs stratify for long periods (Heide, 1982; Tundisi *et al.*, 1993). By providing oxygen, outflow rates and residence times largely determine decomposition of the drowned vegetation and the aging process of the reservoir ecosystem (Tundisi *et al.*, 1993). In Brokopondo Reservoir, with its long 26-month residence time, decomposition of inundated rainforest vegetation took approximately 4 years (Heide, 1982). However, physicochemical stabilization was further delayed by decomposition of a huge biomass of dead floating macrophytes, estimated at 470 ton dry mass per km[2] (Panday-Verheuvel, 1983), that sank to the reservoir bottom after spraying with herbicide in 1969. The time necessary to reach temporal stability in reservoir fish fauna was similar for Brokopondo (14 years) and Kariba (10 years; Balon, 1974) reservoirs. In Petit Saut Reservoir (French Guiana; residence time of 6 months), species composition of the fish fauna was still changing seven years after closure of the dam (Mérona, 2002).

The fish fauna of Brokopondo Reservoir was derived from the Suriname River fish fauna. With the exception of East Africa the tropics have few natural lakes with lacustrine fish species (Fernando & Holèik, 1982) and the fish fauna of Amazonian reservoirs is mainly of riverine origin. In Brokopondo Reservoir, much like other Neotropical reservoirs (Araujo-Lima *et al.*, 1995; Agostinho *et al.*, 1999), the fish community of shore habitat had more species, higher species diversity and higher evenness than the open water community. This may be explained by (1) the greater structural complexity of shore habitat (woody debris, dead bushes, submerged macrophytes) compared to open water habitat and (2) the fact that most riverine fishes have experienced littoral-like conditions in their pre-impoundment habitat (*e.g.* floodplains) and thus tend to stay near the shore when colonizing reservoirs whereas only few species are preadapted to exploit the open water habitat (Fernando & Holèik, 1982). Cichlids, which are known to thrive in tropical lakes and reservoirs (Fernando & Holèik, 1982), were also dominant in the littoral of Brokopondo Reservoir.

The open water habitat of Brokopondo Reservoir had only ten fish species and, with the exception of *Acestrorhynchus*, all open water species were also collected in the shore habitat. The open-water species *S. rhombeus*, *B. melanurus* and *C. ocellaris* should probably return to shore periodically to spawn (*e.g.* Zaret, 1980) and their early stages and small juveniles were collected exclusively in the shore habitat. The important criterion of success as a pelagic open-water species is the ability to feed on zooplankton in the adult period (Fernando, 1994). Tropical freshwaters have only a small number of obligate zooplanktivorous fishes, mainly in the family Clupeidae. Clupeids

Table 5. Comparison of average wet mass per specimen (mean ± SD; g) of some dominant fish species in samples of Suriname River (1963-1964) and Brokopondo Reservoir (2002-2005). Number of samples in parentheses. Results of *t*-test are given. Measurements of wet mass of Suriname River fishes were taken 40 years after the specimens had been placed in ethanol, which is known to cause significant shrinkage of tissues; these values should be taken as minimum values[1].

Species	Suriname River[1] (wet mass per specimen, g)	Brokopondo Reservoir (wet mass per specimen, g)	*p*
Bryconops melanurus	8.3 ± 4.0 (31)	5.5 ± 1.1 (45)	<0.0001
Hemiodus argenteus	18.6 ± 7.0 (9)	13.8 ± 8.8 (21)	0.1604
Hemiodus unimaculatus	28.2 ± 27.7 (21)	25.2 ± 13.4 (32)	0.6013
Crenicichla saxatilis	24.6 ± 16.9 (20)	7.6 ± 3.3 (4)	0.0618
Geophagus surinamensis	28.5 ± 13.5 (33)	13.8 ± 7.3 (8)	0.0052
Guianacara owroewefi	10.2 ± 6.3 (26)	6.5 ± 6.8 (5)	0.2381
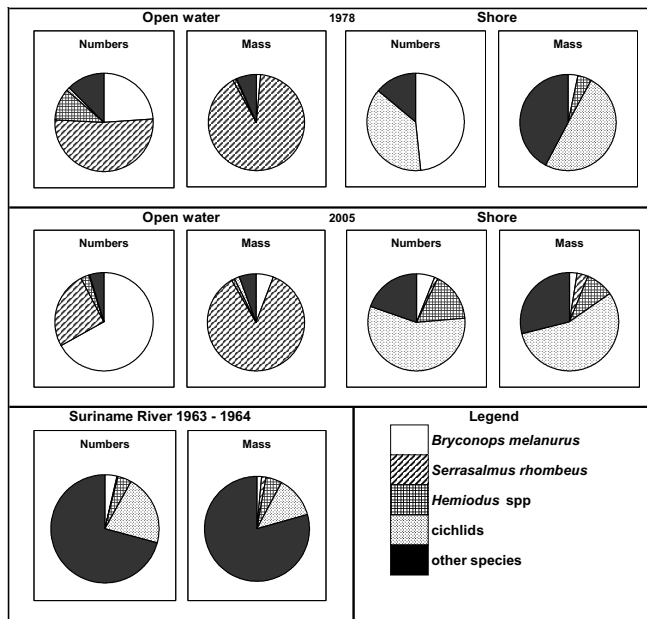
Fig. 3. Fish community structure of Suriname River prior to construction of the dam at Afobaka as compared to fish community structure in open water and forested shore habitats in Brokopondo Reservoir in 1978 (data in Richter & Nijssen (1980) and Kapetsky (1978)) and 2002-2005 (present study). Average proportions (%) in number of specimens and biomass are given for the most abundant species (-groups).

were abundant in open water of African reservoirs (Jackson *et al.*, 1988), but the Amazonian freshwater clupeid *Pellona* was not abundant or even absent in Tucuruí (Leite, 1993), Samuel (Santos, 1995), Curuá-Una (Vieira, 1982) and Petit Saut (Mérona *et al.*, 2003) reservoirs. The catfish *Hypophthalmus* was the only zooplanktivorous fish (Carvalho, 1980) that was abundant in Amazonian reservoirs, *e.g.* in Samuel (Santos, 1995) and Tucuruí (Ribeiro *et al.*, 1995) reservoirs. Facultative zooplanktivorous fishes in Amazonian reservoirs included *Anodus elongatus* (Tucuruí Reservoir), *Anchovia surinamensis* (Tucuruí Reservoir), *Auchenipterus nuchalis* (Curuá-Una and Tucuruí reservoirs), *Triportheus* (Petit Saut Reservoir) and *Hemiodus* spp (Curuá-Una and Tucuruí reservoirs) (Ferreira, 1984; Mérona *et al.*, 2001, 2003). The middle Suriname River had no freshwater clupeids nor *Hypophthalmus* (Appendix 1), whereas *A. surinamensis* (which probably spawns in the estuary), *Triportheus* and *A. nuchalis* did not survive in the reservoir and the two *Hemiodus* species fed exclusively on detritus. In Brokopondo Reservoir, *B. melanurus* was the only fish that fed on zooplankton in open water, but Culicinae pupae and terrestrial invertebrates were also a substantial component in its diet. Riverine *Bryconops* mainly fed on allochthonous invertebrates (*e.g.* Saul, 1975; Mérona *et al.*, 2003) and the reduced body mass of *B. melanurus* in Brokopondo Reservoir as compared to riverine populations may indicate sub-optimal feeding and stunting in the reservoir. Adaptation to a new diet is well documented in reservoir fishes (Jackson *et al.*, 1988), including Amazonian species (Mérona *et al.*, 2001, 2003). In Petit Saut Reservoir, juvenile cichlids *K. guianensis* and *C. saxatilis* had thin bodies when feeding sub-optimally on small-sized

zooplankton (Ponton & Mérigoux, 2000). In the open water of Brokopondo Reservoir, *S. rhombeus* fed on shoals of pelagic *Bryconops* prey, but, piranhas from the reservoir showed reduced standard length as compared to riverine populations.

Food chains in open water of Brokopondo Reservoir were based on autochthonous autotrophic production, fine flocculent detritus of unknown origin and, to a lesser extent, allochthonous production of the rain forest. In Neotropical rivers, the main source of energy is allochthonous organic material (Araujo-Lima *et al.*, 1995), whereas reservoirs are fundamentally autotrophic systems (Baxter, 1977). In reservoirs, allochthonous organic material is probably most important to shore fishes, but in the open water of Brokopondo Reservoir *B. melanurus* and *S. rhombeus* also fed to some extent on food from the forest. Heterotrophic activity based on the decomposition of inundated forest vegetation is dominant in the filling phase of a reservoir (Baxter, 1977; Heide, 1982). A great development of detritivorous fishes was observed in Guri (Novoa *et al.*, 1991), Petit Saut (Mérona *et al.*, 2003) and Itaipu (Agostinho *et al.*, 1999) reservoirs. The high abundance of detritus-feeding *Hemiodus* in Brokopondo Reservoir showed that detritus-based food chains can also be important in later stages of reservoir development. *Macrobrachium* shrimps probably also fed on detritus in Brokopondo and Tucuruí (Tundisi *et al.*, 1993) reservoirs. Relatively long autochthonous food chains in open water of Brokopondo Reservoir (involving phytoplankton and zooplankton, both rare in Suriname River) may partially explain high mercury concentrations in the top predator *S. rhombeus* (up to 4.6 µg Hg per g muscle tissue) as compared to much lower Hg levels in piranhas from contaminated rivers (Mol *et al.*, 2001). At Tucuruí, high mercury levels were detected in reservoir fish (including piranha) and human hair (Aula *et al.*, 1994).

In 172 fish species of the middle Suriname River only 41 were collected in Brokopondo Reservoir 40 years after closure of the dam. The middle reach of Suriname River in the reservoir area may be viewed as a zone with high habitat heterogeneity where headwater and coastal plain species overlap, resulting in high fish diversity. The serial discontinuity concept (Ward & Stanford, 1983, 1995) predicts that a dam in middle reaches can have a large impact on riverine fish diversity. Agostinho *et al.* (1999) pointed out that an unavoidable effect of impoundment on the fish fauna is a shift in species composition and abundance, with extreme proliferation of some species and reduction or elimination of others. Jackson *et al.* (1988) argued that new African reservoirs after a few years had more fish species than were present in the river previous to impoundment, but, if true, this can only be explained by the introduction of exotic species. Jackson *et al.* (1988) also showed that several riverine fishes were not able to adapt to the new conditions and disappeared from the reservoir. In Amazonian reservoirs, the number of fish species was reduced as compared to pre-impoundment faunas: 55 reservoir species vs 214 riverine species in Curuá-Una Reservoir, 127 vs 141 in Tucuruí Reservoir, and 43 vs 126 in Petit Saut Reservoir (Table 6). The number of pre-impoundment fish species for Jamari (122) and Tocantins (141) rivers was probably underestimated by gill net sampling because Santos *et al.* (1984) indicate for Tocantins River a total

number of 300 species collected by diverse gears. The dominance of only two or three fish species in reservoir faunas was reflected in a reduced species diversity and evenness in Brokopondo, Tucuruí and Samuel reservoirs as compared to pre-impoundment river faunas (Table 6).

Fish communities of reservoirs are the result of a restructuring of local riverine communities (Agostinho *et al.*, 1999). The zooplanktivorous catfish *Hypophthalmus* did not occur in the middle Suriname River before impoundment and its absence from Brokopondo Reservoir may well have allowed for the success of *B. melanurus* in open water. In Curuá-Una Reservoir, *Bryconops* was also abundant in the absence of *Hypophthalmus*, whereas in Petit Saut Reservoir the zooplanktivorous niche was occupied by *Triportheus* (Table 6). Piranhas (*Serrasalmus* spp) and peacock cichlids (*Cichla* spp) were highly successful in Amazonian reservoirs (including Brokopondo), but they did not occur in Sinnamary River and consequently they were also absent from Petit Saut Reservoir (Table 6). Other predatory fishes that were successful in Amazonian reservoirs include *Acestrorhynchus*, *Hoplias*, *Plagioscion*, *Boulengerella* and *Hydrolycus* (Table 6; the latter two genera absent from Suriname River and Brokopondo Reservoir).

Large migratory catfishes of Suriname River (*B. filamentosum*, *H. platyrhynchos* and *P. fasciatum*) were not collected in Brokopondo Reservoir in 1978 and 2002-2005. Many large-sized migratory catfishes are mainstays of Neotropical subsistence and commercial river fisheries, but they are vulnerable to damming because of their wide-ranging habits (Barthem *et al.*, 1991; Araujo-Lima *et al.*, 1995; Agostinho *et al.*, 1999; Carolsfeld *et al.*, 2003). However, different species react to damming differently and some may be able to survive in the smaller sections of river that are available to them after a dam is erected. In Tucuruí (Ribeiro *et al.*, 1995) and Itaipu (Agostinho *et al.*, 1999) reservoirs, large migratory catfishes - after initial increase based on populations upstream of the reservoir - became rare. However, *Pterodoras granulosus* was able to extend its distribution from the Lower and Middle Paraná to Upper Paraná and Itaipu Reservoir after the reservoir inundated the natural barrier of Sete Quedas Falls (Agostinho *et al.*, 1999).

Potamodromous detritivorous characoids were more successful in Amazonian reservoirs than piscivorous migratory catfishes. In Brokopondo Reservoir, *P. rubrotaeniatus* was collected in both 1978 (Richter & Nijssen, 1980) and 2002-2005 (present study). In Guri (Novoa *et al.*, 1991) and Tucuruí (Ribeiro *et al.*, 1995) reservoirs, the decomposing inundated vegetation became a major feeding habitat for *Semaprochilodus* and *Prochilodus* and important fisheries targeted these species both in the reservoir and during their upriver spawning runs. Nijssen (1969) observed a shoal of *Prochilodus* leaving Brokopondo Reservoir moving up the Suriname River (where it is important in subsistence fisheries). However, downstream of the dam *Prochilodus* virtually disappeared from Tocantins (Ribeiro *et al.*, 1995) and Suriname (E. Fonkel, pers. comm.) rivers.

Rheophylic fishes adapted to fast currents in rapids did not survive in non-flowing water of Brokopondo Reservoir (present study) and African reservoirs (Jackson *et al.*, 1988). Rapid-dwelling fishes occurred in Sinnamary River (Horeau

et al., 1998) but were not collected in Petit Saut Reservoir (BdM, unpublished data). Fishes from other specific riverine habitats like sandy beaches, submerged leaf litter, woody debris and low-order headwater streams would probably not survive impoundment because their habitat is drowned in the reservoir. Examples of Suriname River habitat specialists that did not survive in Brokopondo Reservoir include *Gymnorhamphichthys* (burrows in sandy bottoms), small-sized characoids, catfishes and cichlids from leaf litter, and *Ancistrus* from woody debris. A case in point is the miniature catfish *Lithoxus pallidimaculatus* (36-46 mm SL), endemic to the Suriname River basin and known only from four specimens collected in a first-order tributary of Sara Creek (Boeseman, 1982), which may now be at risk of extinction or already extinct after inundation of its collection locality.

Brokopondo Reservoir, like the first great African impoundments, was a genuine novelty and there was no basis in experience on which to predict its consequences (Leentvaar, 1973). Subsequent Amazonian reservoirs had similar short-term environmental (Fearnside, 2001) and social (Fearnside, 1999) impacts. The long-term impact of Brokopondo Dam on the pre-impoundment riverine fish fauna was a drastic decrease in number of species, species diversity and evenness. Forty years after closure of the dam, some mammals of the rainforest were still negatively affected by the reservoir as revealed by the drowning of peccaries and other species that try to swim across the large reservoir (F. van Troon, pers. communication). Commercial fisheries, often a positive effect of tropical reservoirs (Jackson, 1975), never developed on Brokopondo Reservoir (Kapetsky, 1978) probably because the most abundant large-sized species, *S. rhombeus*, destroys gill nets and is not an appreciated food fish in Suriname. High mercury levels in predatory fishes from Brokopondo Reservoir (Mol *et al.*, 2001), associated with a recent (1990s) boom in small-scale gold mining, pose a serious health problem to Maroon people in the reservoir area (*e.g.* Brownsweg) and affect sport fishing on peacock cichlid *Cichla*. Migratory fishes can transport bioaccumulated mercury from the reservoir to villages along the upper Suriname River.

We are aware that hydropower can be a solution for the energy demand of future projects in Suriname (*e.g.* Kabalebo River project) and Amazonia, but a small catchment and flat topography results in large reservoirs that generate little power (low MW/km^2) such as Balbina (Brazil) and Brokopondo reservoirs. Reservoir construction is never warranted without prior assessment of alternatives based on scientific knowledge (Ackerman *et al.*, 1973). Adverse effects in the reservoir area, downstream of the dam and in upper parts of the watershed should be prevented, mitigated or compensated. Since the construction of Brokopondo Reservoir and the large African reservoirs in the 1950s and 1960s, sustainability of economic development has become top priority in the policy of the World Bank (Goodland, 1990) and, consequently, the World Bank refused to finance construction of the Tucuruí Dam because environmental problems were not adequately addressed (Fearnside, 2001). A rational approach to long-term sustainable use of natural resources in a watershed should include ecological zoning and integration of all ecological

Table 6. Relative abundance in numbers (N, %) and biomass (M, %) of dominant reservoir fishes in pre- and post-impoundment studies of Amazonian reservoirs; nc = not collected during study; np = not present in pre-impoundment riverine fauna. Source of data: Brokopondo Reservoir (present study), Guri Reservoir (Alvarez *et al*., 1986; Novoa *et al*., 1991), Curuá-Una Reservoir (Vieira, 1982), Tucuruí Reservoir (Leite, 1993), Samuel Reservoir (Santos, 1995), Petit Saut Reservoir (Tito de Morais & Lauzanne, 1994; Mérona *et al*., 2003). No data are available of the fish fauna in the Guri Reservoir area before closure of the dam[1]. No pre-impoundment data for Curua-Una dam are available; presented are data of the fish fauna of the Curua-Una River up- and downstream of dam[2]. Later in time (1982-1983), Ferreira (1984) found *Hemiodus* spp together with *Auchenipterus* and *Serrasalmus* dominant in number of specimens in Curua-Una Reservoir[3]. Piranha species in Tucuruí Reservoir included the redbelly piranha *Pygocentrus nattereri*[4]. Santos *et al*. (1984) indicate a total number of 300 species collected by diverse gears in Tocantins River[5].

Reservoir characteristics

Reservoir	Brokopondo	Guri	Curuá-Una	Tucuruí	Samuel	Petit-Saut
Country	Suriname	Venezuela	Brazil	Brazil	Brazil	French Guiana
River	Suriname	Caroni	Curuá-Una	Tocantins	Jamari	Sinnamary
Year of closure of dam	1964	1968	1977	1984	1988	1994
Surface area (km^2)	1560	4300	87	2430	580	350
Residence time (months)	26	?	1	1.7	?	6
Reservoir age in post-impoundment study (years)	40	16	1	1-3	3-4	0-7

Fish community structure

Taxon	Mpre	Npre	Mpost	Npost	Mpost[1]	Nriv[2]	Npost	Npre	Npost	Npre	Npost	Mpre	Mpost
Bryconops spp.	1.5	3.6	5.3	36.6	0.0	32.4	23.3	0.0	0.5	0.0	0.0	5.6	4.8
Triportheus spp.	0.4	0.1	0.0	0.0	nc	0.3	0.0	5.8	5.1	0.0	0.0	9.1	39.6
Hemiodus spp.	5.0	4.0	6.1	18.9	0.0	5.4	0.1[3]	13.3	8.2	0.0	1.0	4.6	1.6
Prochilodus spp.	0.13	0.04	1.35	0.11	63.3	nc		0.7	1.6	6.4	0.0	np	
Acestrorhynchus spp.	3.4	2.3	2.6	1.6	0.0	7.6	34.4	0.4	3.1	0.0	4.0	13.0	8.6
Boulengerella spp.	np				nc	4.4	4.9	4.0	3.0	1.9	0.0	np	
Charax spp.	0.6	0.9	0.0	0.1	0.0	1.7	6.3	0.0	0.0	nc		0.4	4.8
Hydrolycus spp.	np				10.3	0.5	0.0	2.5	5.1	6.3	0.0	np	
Hoplias spp.	2.6	1.1	0.9	1.0	3.4	0.3	0.3	0.0	0.0	2.5	0.0	26.9	5.0
Serrasalmus spp.	1.4	0.4	67.7	11.8	2.4	3.9	11.6	1.1	29.9[4]	0.0	54.3	np	
Auchenipterus spp.	0.0	0.1	0.0	0.0	0.0	6.8	5.5	10.6	1.7	0.0	0.0	2.8	4.6
Hypophthalmus spp.	np				nc	nc		0.0	0.3	0.0	16.0	np	
Trachelyopterus galeatus	0.3	1.0	0.0	0.0	0.0	0.3	1.5	0.0	4.4	0.0	2.0	0.3	11.9
Cichla spp.	1.6	1.5	2.8	3.2	5.7	0.2	1.9	0.5	5.1	0.0	9.0	np	
Geophagus spp.	4.9	5.6	2.8	7.1	0.2	0.1	1.3	1.1	0.7	4.1	0.0	0.1	0.0
Plagioscion spp.	0.1	0.1	1.1	0.1	10.8	0.0	0.0	0.6	1.0	0.0	0.3	0.0	0.0
Total	21.9	20.7	90.6	80.5	96.1	63.9	91.1	40.6	69.7	21.5	86.3	62.8	80.9
Number of species *S*	172		41		58	214	55	141[6]	127	122		126	43
Species diversity *H*	3.76	4.11	1.53	2.17				4.7	3.4	3.09	1.61		2.9
Evenness *J*	0.74	0.80	0.42	0.60				0.78	0.67	0.81	0.55		0.7

and socio-economic implications into an overall River Basin Plan (Ribeiro *et al.*, 1995).

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Appendix 1. Fish community structure of Suriname River in future Brokopondo Reservoir area (i.e. upstream of the first rapids at Phedra; 135 km from the estuary) in 1963-1964 (collection of M. Boeseman in Naturalis Museum, Leiden, The Netherlands) and Brokopondo Reservoir in 1966-1967 (presence/absence only; Nijssen, 1967, 1969; Richter & Nijssen, 1980), 1978 (Kapetsky, 1978; Richter & Nijssen, 1980) and 2002-2005 (present study) in proportion of number of specimens (N) and wet mass (M). Number of samples in parentheses. Community structure of shore habitat in 1978 is based on one sample (Kapetsky, 1978) for number of specimens, but three samples for wet mass[1]. Also given are number of species, Shannon-Wiener index of species diversity (*H*) and evenness (*J*). Fishes endemic to the Suriname River basin are denoted with an asterisk. The fish species *H. aimara*, *S. eigenmanni*, *P. squamosissimus* and *P. surinamensis* were caught in Brokopondo Reservoir in 2000 by Mol *et al.* (2001)[2]. The large catfish *Brachyplatystoma filamentosum* was photographed by Boeseman at Brokopondo in February 1964 (see Mees, 1974, Plate 15); the specimen is identified as *B. vaillantii* in Mees (1974), but taking into account its large size (170 cm TL) this should be *B. filamentosum*; here we use a conservative estimate of its weight (30 kg; see length-weight relationship at http://www.fishbase.org W = 0.0102*TL^3) [3]. Richter & Nijssen (1980) probably misidentified *Pimelodus blochii* as *Pimelodus albofasciatus* Mees, 1974[4] , *Crenicichla multispinosa* as *Crenicichla lugubris* Heckel, 1840[5], and *Guianacara owroewefi* as *Guianacara geayi* (Pellegrin, 1902)[6]. Tarpon *M. atlanticus* is a catadromous species which was observed in the Suriname River as far upstream as Berg en Dal (km 165) (Mees, 1967)[7]. The guppy *M. bifurca* was observed in Suriname River (Boeseman, 1964) and Brokopondo Reservoir (Nijssen, 1967)[8]. The biomass of the shore community in 1978 is expressed in kg per ha[9].

	Suriname River		1966 1967	Brokopondo Reservoir																	
	1963-1964 (115)			1978						2002-2005											
				Open water (2)		Shore (3)[1]		Total (3/5)[1]		Open water (17)		Shore (5)		Bay (25)		Beach (7)		Total (54)			
Order, family, species	N (%)	M (%)		N (%)	M (%)	N (%)	M (%)	N (%)	M (%)	N (%)	M (%)	N (%)	M (%)	N (%)	M (%)	N (%)	M (%)	N (%)	M (%)		
Characiformes	**58.23**	**44.87**		**92.68**	**98.92**	**52.97**	**36.30**	**79.80**	**62.51**	**99.61**	**98.22**	**42.07**	**36.88**	**98.17**	**94.52**	**85.84**	**63.16**	**77.71**	**91.39**		
Anostomidae	**2.10**	**4.09**		**0.00**	**0.00**	**0.00**	**2.60**	**0.00**	**1.30**	**0.00**	**0.00**	**0.13**	**2.20**	**0.94**	**2.15**	**0.00**	**0.00**	**0.34**	**1.15**		
Anostomus anostomus	0.05	0.02					0.01		0.01												
Leporinus aff. *cylindriformis*	0.02	0.04																			
Leporinus fasciatus	0.38	1.15	x				1.20		0.55			0.09	1.01	0.54	0.67			0.20	0.39		
Leporinus friderici	0.95	1.83	x				1.20		0.55			0.04	1.19					0.02	0.10		
Leporinus gossei	0.01	0.00																			
Leporinus cf. *lebaili*	0.03	0.22																			
Leporinus nijsseni	0.55	0.77																			
Leporinus pellegrinii	0.10	0.04					0.19		0.19												
Schizodon fasciatus	0.02	0.01	x											0.40	1.48			0.12	0.66		
Characidae	**36.76**	**17.10**		**31.22**	**2.25**	**52.18**	**6.95**	**36.17**	**4.84**	**71.28**	**9.73**	**15.59**	**4.09**	**53.03**	**7.52**	**39.94**	**20.94**	**42.78**	**9.18**		
Acestrorhynchus falcatus	0.39	1.02	x			0.79	0.19	0.26	0.10	0.40	0.37			0.35	0.46			0.20	0.37		
Acestrorhynchus microlepis	1.90	2.33	x	1.99	0.13		0.03	1.29	0.07	4.04	3.62			1.34	1.26			1.36	2.19		
Astyanax bimaculatus	0.61	0.33																			
Astyanax spp.	0.16	0.01																			
Brachychalcinus orbicularis	1.54	0.19	x																		
Brycon falcatus	0.74	2.02					0.01		0.01					0.05	0.18			0.02	0.08		
Bryconamericus aff. *stramineus*	0.02	0.00																			
Bryconops affinis	0.03	0.01																			
Bryconops caudomaculatus	0.06	0.01																			
Bryconops melanurus	3.48	1.47	x	26.24	1.16	48.57	3.65	31.99	2.50	66.84	5.74	6.24	2.46	48.51	4.92	36.64	14.08	36.56	5.28		
Chalceus macrolepidotus	0.70	1.48	x				2.31		1.30			0.39	0.96	0.20	0.21			0.20	0.18		
Charax gibbosus	0.90	0.58	x				0.01		0.01					0.15	0.01			0.05	0.01		
Cynodon meionactis	0.05	0.57		2.99	0.96		0.01	1.70	0.44					0.10	0.10			0.03	0.05		
Cynopotamus essequibensis	0.17	0.26																			
Hemigrammus bellottii	1.00	0.01																			
Hemigrammus boesemani	1.38	0.03										8.49	0.31					3.03	0.03		
Hemigrammus spp.	0.12	0.00	x																		
Hemigrammus unilineatus	0.05	0.00																			
Hyphessobrycon simulatus	1.12	0.01																			
Jupiaba abramoides	0.32	0.07	x																		
Jupiaba keithi	2.05	0.49																			
Jupiaba meunieri	0.32	0.06																			
Jupiaba pinnata	0.02	0.00																			
Jupiaba polylepis	2.77	0.35	x			2.82	0.68	0.93	0.37			0.04	0.01	0.05	0.00			0.03	0.00		
Moenkhausia chrysargyrea	0.28	0.13	x																		
Moenkhausia collettii	0.33	0.03																			
Moenkhausia georgiae	0.21	0.27																			
Moenkhausia grandisquamis	4.45	1.80	x							0.04	0.07	0.50	0.16	3.30	6.86	0.49	0.22				

Appendix 1. Cont.

	Suriname River			Brokopondo Reservoir															
				1978						2002-2005									
	1963-1964 (115)		1966 1967	Open water (2)		Shore (3)[1]		Total (3/5)[1]		Open water (17)		Shore (5)		Bay (25)		Beach (7)		Total (54)	
Moenkhausia hemigrammoides	1.14	0.04																		
Moenkhausia lepidura	0.02	0.00																		
Moenkhausia oligolepis	4.08	1.52	x				0.03		0.02											
Moenkhausia spp.	0.01	0.00																		
Moenkhausia surinamensis	0.08	0.07																		
Phenacogaster aff. *microstictus*	0.58	0.01																		
Piabucus dentatus	0.06	0.03																		
Poptella brevispina	3.26	0.96	x				0.03		0.02				0.35	0.27	1.04	0.12			0.45	0.08
Pristella maxillaris	0.29	0.01																		
Roeboexodon guyanensis	0.13	0.02																		
Roeboides thurni	0.04	0.02	x										0.04	0.01	0.74	0.10			0.25	0.05
Tetragonopterus chalceus	1.78	0.54	x																	
Triportheus brachipomus	0.10	0.37																		
Crenuchidae	**0.35**	**0.01**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Characidium zebra	0.02	0.00																		
Crenuchus spilurus	0.01	0.00																		
Melanocharacidium dispilomma	0.18	0.01																		
Microcharacidium eleotrioides	0.14	0.00																		
Curimatidae	**6.29**	**9.13**		**0.00**	**0.00**	**0.00**	**4.24**	**0.00**	**3.81**	**0.07**	**0.23**	**0.00**	**0.00**	**0.79**	**3.51**	**0.00**	**0.00**	**0.26**	**1.67**
Caenotropus labyrinthicus	0.26	0.84																		
Curimata cyprinoides	2.27	6.56	x							0.07	0.23			0.79	3.51			0.26	1.67
Curimatella alburna	0.09	0.11	x																	
Cyphocharax helleri	0.48	0.25	x																	
Cyphocharax spilurus	3.10	1.32	x				4.24		3.81											
Steindachnerina varii	0.09	0.04																		
Erythrinidae	**1.24**	**2.99**		**0.00**	**0.00**	**0.79**	**16.46**	**0.26**	**10.70**	**0.00**	**0.00**	**2.73**	**10.94**	**0.00**	**0.00**	**0.00**	**0.00**	**0.97**	**0.91**
Erythrinus erythrinus	0.17	0.16	x																	
Hoplerythrinus unitaeniatus	0.02	0.25	x																	
Hoplias aimara	0.42	1.21	x																x[2]	
Hoplias malabaricus	0.63	1.37	x			0.79	16.46	0.26	10.70			2.73	10.94					0.97	0.91
Gasteropelecidae	**4.96**	**0.68**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Carnegiella strigata	0.02	0.00	x																	
Gasteropelecus sternicla	4.94	0.68	x																	
Hemiodontidae	**4.61**	**5.26**		**10.63**	**0.90**	**0.00**	**5.61**	**6.91**	**3.27**	**2.58**	**1.04**	**22.71**	**15.88**	**25.64**	**9.22**	**45.59**	**37.96**	**21.17**	**6.71**
Bivibranchia bimaculata	0.51	0.28																		
Bivibranchia simulata	0.07	0.02										6.20	6.94	0.15	0.02	0.63	0.88	2.32	0.61
Hemiodus argenteus	0.58	0.58								0.26	0.05	16.29	8.37	18.66	6.09	44.65	36.06	16.08	4.20
Hemiodus unimaculatus	3.45	4.38	x	10.63	0.90		5.61	6.91	3.27	2.32	0.99	0.22	0.57	6.83	3.11	0.31	1.02	2.78	1.90
Lebiasinidae	**0.30**	**0.02**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Copella arnoldi	0.01	0.00																		
Copella carsevenennsis	0.01	0.00																		
Nannostomus beckfordi	0.01	0.00																		
Nannostomus bifasciatus	0.17	0.01																		
Pyrrhulina filamentosa	0.11	0.01	x																	
Prochilodontidae	**0.04**	**0.13**		**1.33**	**2.31**	**0.00**	**0.40**	**0.83**	**1.28**	**0.13**	**0.91**	**0.00**	**0.00**	**0.25**	**2.12**	**0.00**	**0.00**	**0.11**	**1.35**
Prochilodus rubrotaeniatus	0.04	0.13		1.33	2.31		0.40	0.83	1.28	0.13	0.91			0.25	2.12			0.11	1.35
Serrasalmidae	**1.58**	**5.46**		**49.50**	**93.46**	**0.00**	**0.04**	**35.63**	**37.31**	**25.55**	**86.31**	**0.91**	**3.77**	**17.52**	**70.00**	**0.31**	**4.26**	**12.08**	**70.42**
Acnodon oligacanthus	0.55	0.42																		
Myleus rhomboidalis	0.37	0.98																		
Myleus ternetzi	0.14	0.45																		
Myloplus rubripinnis	0.15	1.85		1.66	2.21		0.04	0.94	1.02	0.07	0.35			0.94	5.73			0.31	2.72
Serrasalmus eigenmanni	x[2]																		x[2]	
Serrasalmus rhombeus	0.36	1.40	x	47.84	91.25			34.68	36.29	25.48	85.96	0.91	3.77	17.52	64.27	0.31	4.26	11.77	67.70
Tometes lebaili	0.02	0.38																		
Gymnotiformes	**2.25**	**2.63**		**0.00**	**0.00**	**1.63**	**1.01**	**0.54**	**0.55**	**0.00**	**0.00**	**0.22**	**0.41**	**0.00**	**0.00**	**0.00**	**0.00**	**0.08**	**0.03**
Apteronotidae	**0.17**	**0.06**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Apteronotus albifrons	0.17	0.06																		
Gymnotidae	**0.31**	**1.35**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Electrophorus electricus	0.05	0.98	x																	
Gymnotus anguillaris	0.06	0.01																		
Gymnotus carapo	0.19	0.35	x																	

Appendix 1. Cont.

	Suriname River			Brokopondo Reservoir															
				1978						2002-2005									
	1963-1964 (115)		1966 1967	Open water (2)		Shore (3)[1]		Total (3/5)[1]		Open water (17)		Shore (5)		Bay (25)		Beach (7)		Total (54)	
Hypopomidae	**0.26**	**0.13**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Brachyhypopomus beebei	0.08	0.02																	
Hypopomus artedi	0.15	0.10																	
Hypopomus sp.	-		x																
Hypopygus lepturus	0.03	0.01																	
Rhamphichthyidae	**0.02**	**0.01**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Gymnorhamphichthys rondoni	0.02	0.01																	
Sternopygidae	**1.49**	**1.08**		**0.00**	**0.00**	**1.63**	**1.01**	**0.54**	**0.55**	**0.00**	**0.00**	**0.22**	**0.41**	**0.00**	**0.00**	**0.00**	**0.00**	**0.08**	**0.03**
Eigenmannia aff. *virescens*	1.27	0.69																	
Sternopygus macrurus	0.22	0.39				1.63	1.01	0.54	0.55			0.22	0.41					0.08	0.03
Siluriformes	**16.78**	**37.23**		**6.31**	**0.56**	**8.09**	**10.85**	**6.34**	**5.95**	**0.00**	**0.00**	**0.99**	**1.83**	**0.00**	**0.00**	**0.00**	**0.00**	**0.36**	**0.15**
Aspredinidae	**0.58**	**0.11**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Bunocephalus amaurus	0.58	0.11																	
Auchenipteridae	**1.18**	**0.31**		**5.98**	**0.41**	**0.00**	**0.01**	**3.39**	**0.20**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Auchenipterus nuchalis	0.09	0.03		5.98	0.41		0.01	3.39	0.20										
Centromochlus punctatus	0.03	0.01																	
Pseudauchenipterus nodosus	0.02	0.00																	
Tatia brunnea	0.07	0.02																	
Trachelyopterus galeatus	0.96	0.25	x																
Callichthyidae	**2.08**	**2.38**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Callichthys callichthys	0.40	0.47	x																
Corydoras aeneus	0.09	0.01																	
Corydoras boesemani	0.12	0.01																	
Corydoras geoffroy	0.02	0.00																	
Corydoras nanus	0.04	0.00																	
Corydoras punctatus	0.93	0.10	x																
Megalechis thoracata	0.48	1.79	x																
Cetopsidae	**0.10**	**0.01**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Helogenes marmoratus	0.10	0.01																	
Doradidae	**1.56**	**3.11**		**0.00**	**0.00**	**0.79**	**1.81**	**0.26**	**1.12**	**0.00**	**0.00**	**0.04**	**0.20**	**0.00**	**0.00**	**0.00**	**0.00**	**0.02**	**0.02**
Doras carinatus	0.50	0.82																	
Platydoras dentatus	1.06	2.29				0.79	1.81	0.26	1.12			0.04	0.20					0.02	0.02
Heptapteridae	**5.49**	**2.17**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.04**	**0.03**	**0.00**	**0.00**	**0.00**	**0.00**	**0.02**	**0.00**
Chasmocranus longior	0.29	0.05																	
*Chasmocranus surinamensis**	0.02	0.01																	
Imparfinis cf. *minutus*	0.02	0.01																	
Imparfinis pijpersi	0.15	0.02																	
Pimelodella cristata	4.70	1.94	x																
Rhamdia quelen	0.31	0.14	x									0.04	0.03					0.02	0.00
Loricariidae	**4.12**	**4.04**		**0.33**	**0.15**	**7.30**	**9.02**	**2.68**	**5.62**	**0.00**	**0.00**	**0.91**	**1.60**	**0.00**	**0.00**	**0.00**	**0.00**	**0.32**	**0.13**
Ancistrus aff. *leucostictus*	0.03	0.03																	
Ancistrus temminckii	0.77	0.30																	
Cteniloricaria maculata	0.01	0.00																	
Harttia surinamensis	0.46	0.02																	
Hypostomus gymnorhynchus	0.03	0.02																	
*Hypostomus micromaculatus**	0.04	0.15																	
*Hypostomus paucimaculatus**	0.02	0.01																	
Hypostomus plecostomus	0.02	0.03	x																
*Hypostomus surinamensis**	0.30	1.72	x									0.13	0.29					0.05	0.02
Hypostomus ventromaculatus	0.07	0.09	x	0.33	0.15	7.30	9.02	2.68	5.62										
*Lithoxus pallidimaculatus**	0.05	0.00																	
Lithoxus surinamensis	0.82	0.01																	
Loricaria cataphracta	0.29	0.23																	
Loricariichthys maculatus	0.16	0.26	x									0.78	1.31					0.28	0.11
Metaloricaria nijsseni	0.12	0.15																	
Pseudancistrus barbatus	0.37	1.54																	
Pseudancistrus brevispinis	0.40	0.48																	
Rineloricaria stewarti	0.18	0.02	x																

Appendix 1. Cont.

| | Suriname River | | | Brokopondo Reservoir | | | | | | | | | | | | | | | |
| | 1963-1964 (115) | | 1966 1967 | 1978 | | | | | | 2002-2005 | | | | | | | | | |
				Open water (2)		Shore (3)[1]		Total (3/5)[1]		Open water (17)		Shore (5)		Bay (25)		Beach (7)		Total (54)	
Pimelodidae	**0.84**	**25.05**		**0.00**	**0.00**	**0.00**	**0.01**	**0.00**	**0.01**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Brachyplatystoma filamentosum[3]	0.01	17.01																	
Hemisorubim platyrhynchos	0.03	0.14	x																
Pimelodus blochii	0.30	0.46					0.01[4]		0.01										
Pimelodus ornatus	0.49	2.90																	
Pseudoplatystoma fasciatum	0.01	4.54	x																
Pseudopimelodidae	**0.63**	**0.04**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Batrochoglanis raninus	0.02	0.01	x																
Microglanis poecilus	0.56	0.01	x																
Microglanis secundus	0.03	0.00																	
Pseudopimelodus bufonius	0.02	0.02																	
Trichomycteridae	**0.20**	**0.01**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Ituglanis amazonicus	0.06	0.00																	
Ochmacanthus aff. *flabelliferus*	0.14	0.01																	
Perciformes	**21.45**	**12.97**		**0.99**	**0.51**	**38.07**	**51.81**	**13.32**	**29.97**	**0.40**	**1.78**	**56.68**	**56.00**	**0.89**	**5.47**	**14.00**	**17.81**	**21.94**	**8.27**
Cichlidae	**21.05**	**12.78**		**0.99**	**0.51**	**38.07**	**51.81**	**13.32**	**29.97**	**0.40**	**1.78**	**56.68**	**56.00.**	**0.59**	**2.93**	**14.00**	**17.81**	**21.85**	**7.13**
Aequidens tetramerus	0.02	0.03	x																
Apistogramma steindachneri	0.83	0.04	x																
Cichla ocellaris	1.52	1.60	x	0.33	0.01	7.70	34.00	2.73	18.16	0.40	1.78	6.54	5.90	0.54	2.92	6.13	8.27	3.20	2.77
Cichlasoma bimaculatum	3.49	0.79	x			0.65	2.50	0.22	2.00			2.47	2.52					0.88	0.21
Crenicichla multispinosa	0.11	0.21					0.50[5]		0.30			0.78	1.03			0.16	0.18	0.29	0.09
Crenicichla saxatilis	2.20	2.11	x				0.63		0.30			2.43	2.55					0.86	0.21
Geophagus surinamensis	5.65	4.93	x	0.66	0.50	28.37	9.02	9.92	4.97			17.85	31.46	0.05	0.01	7.55	9.34	7.12	2.81
Guianacara owroewefi	4.14	1.71	x[6]			0.65	2.50	0.22	2.10			23.27	6.30			0.16	0.02	8.31	0.52
Krobia guianensis	2.60	1.35	x			0.70	2.66	0.23	2.14			3.34	6.24					1.19	0.52
Nannacara anomala	0.51	0.02	x																
Nandidae	**0.31**	**0.01**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Polycentrus schomburgkii	0.31	0.01	x																
Sciaenidae	**0.09**	**0.18**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.30**	**2.54**	**0.00**	**0.00**	**0.09**	**1.14**
Pachypops fourcroi	0.04	0.07																	
Plagioscion auratus	0.04	0.08																x[2]	
Plagioscion squamosissimus	x[2]													0.30	2.54			0.09	1.14
Plagioscion surinamensis	0.02	0.04																x[2]	
Miscellaneous groups	**1.32**	**2.33**		**0.00**	**0.00**	**0.00**	**0.03**	**0.00**	**0.02**	**0.00**	**0.00**	**0.04**	**4.87**	**0.00**	**0.00**	**0.16**	**19.05**	**0.03**	**0.81**
Achiridae	**0.02**	**0.01**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Apionichthys dumerili	0.02	0.01																	
Belonidae	**0.63**	**0.35**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Potamorrhaphis guianensis	0.63	0.35																	
Rivulidae	**0.16**	**0.01**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Rivulus agilae	0.01	0.00																	
Rivulus aff. *holmiae*	0.09	0.01																	
Rivulus aff. *urophthalmus*	0.04	0.00																	
Rivulus spp.	0.02	0.00																	
Engraulididae	**0.30**	**0.11**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Anchovia surinamensis	0.25	0.04																	
Anchoviella lepidentostole	0.02	0.01																	
Lycengraulis batesii	0.03	0.06																	
Megalopidae				**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Megalops atlanticus	x[7]																		
Poeciliidae				**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Micropoecilia bifurca	x[8]		x[8]																
Potamotrygonidae	**0.12**	**1.78**		**0.00**	**0.00**	**0.00**	**0.03**	**0.00**	**0.00**	**0.00**	**0.00**	**0.04**	**4.87**	**0.00**	**0.00**	**0.16**	**19.05**	**0.00**	**0.81**
Potamotrygon orbignyi	0.12	1.78										0.04	4.87			0.16	19.05	0.03	0.81
Synbranchidae	**0.10**	**0.06**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Synbranchus marmoratus	0.10	0.06	x				0.03		0.02										
total number of specimens / biomass (kg)	12842	176.4		301	67.9	2540	26.0[9]	2841	-	1511	110.9	2308	20.5	2020	110.5	636	5.2	6475	247.1
total number of species	172		62	11		31		35		10		27		23		11		41	
Species diversity H	4.11	3.76		1.49	0.46	1.48	2.26	1.82	2.04	0.88	0.62	2.29	2.43	1.58	1.51	1.31	1.81	2.17	1.53
Evenness J	0.80	0.74		0.62	0.19	0.60	0.65	0.75	0.61	0.38	0.27	0.70	0.74	0.51	0.48	0.54	0.75	0.60	0.42