Environmental Biology of Fishes **71:** 33–51, 2004.

Seasonal and habitat influences on fish communities within the lower Yasuni River basin of the Ecuadorian Amazon

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Received 6 May 2002 Accepted 20 December 2003

Key words: neotropical, community structure, floodplain, piscivore–transparency–morphometry (PTM) model

Synopsis

We sampled lagoon, river and forest stream habitats during the rising water, wet, falling water, and dry seasons in the lowland region of the Yasuni National Reserve in the Ecuadorian Amazon. We collected 195 species, increasing the current number of species for the Napo River basin to approximately 562. The steady rate of species accumulation per sample suggests that the fish fauna is still undersampled. Lagoon, river and forest stream fish communities are highly diverse and variable, composed of common species found within several habitats, of characteristic species found throughout the year, and of seasonally migrating species. Characteristic lagoon species were mainly the curimatids *Curimata vittata*, *Psectrogaster amazonica*, *Potamorhina altamazonica*, *P. latior* and *Cyphocharax plumbeus*. The characins *Hyphessobrycon copelandi* and *Hemigrammus* cf. *lunatus* and the catfishes *Nemadoras humeralis*, *Pimelodella* sp. C and *Sorubim* sp. A were characteristic river species. Characteristic forest stream species included *Hoplias malabaricus*, *Hyphessobrycon copelandi*, *Pimelodella* sp. B and *Sternopyugus macrurus*. During the dry season, lagoon and river habitats had the highest number of individuals and species, as fishes were concentrated in decreasing habitat area. In contrast, stream habitats had the highest species richness and abundance during the rising water and falling water seasons. Species collected included vital food fishes and seasonal migrants. The migratory catfishes *Brachyplatystoma vaillantii*, *Hemisorubim platyrhynchos*, *Platynematichthys notatus*, *Platystomatichthys sturio* and *Sorubim lima* were collected during the falling water season, which suggests that these species may begin migrating earlier than expected. These findings highlight the importance of seasonality for both adequately assessing aquatic biodiversity and for developing research and conservation programs encompassing whole river ecosystems.

Introduction

The flood pulse concept by Junk et al. (1989) proposes that a river, its catchment area, and its floodplain are an ecological unit, and that the majority of riverine production stems from production and nutrient recycling within the floodplain. Thus, species adaptations and life history characteristics suited to flood pulses may be reflected in community structure (Junk et al. 1989). Species collected at a particular site represent a subset of a much larger pool of species. During the dry season, communities may include fishes trapped in a contracting aquatic environment (Lowe-McConnell 1987). While during the wet season, communities may include migratory fishes taking advantage of expanding food and habitat resources. A community can be defined as individuals occurring at the same place and time. This is an ecological entity (Saint-Paul et al. 2000) reflecting the area's floodplain with seasonally expanding and contracting aquatic environment.

Studies on spatial and temporal variation in neotropical fish communities have focused on river (Goulding et al. 1988, Ibarra & Stewart 1989, Boujard 1992, Jepsen 1997, Stewart et al. 2002), stream (Henderson & Walker 1990, Mérigoux et al. 1998, 1999, Almirón et al. 2000) and lake habitats (Rodríguez & Lewis 1994, 1997, Galacatos et al. 1996, Henderson & Crampton 1997, Tejerina-Garro et al. 1998, Saint-Paul et al. 2000, Vono & Barbosa 2001). In addition, studies have investigated lagoon fishes found within floating macrophyte habitats (Henderson & Hamilton 1995, Meschiatti et al. 2000), differences among habitats within a localized area (Cox Fernandes 1997, Saint-Paul et al. 2000, Silvano et al. 2000, Petry et al. 2003), and differences between natural and flow-regulated rivers (Mérigoux & Ponton 1999). Fish communities within floodplain rivers and lakes are influenced not only by water type (Marlier 1967, Galacatos et al. 1996, Saint-Paul et al. 2000) but also by turbidity, substrate, pH, depth and flow (Goulding et al. 1988, Ibarra & Stewart 1989, Boujard 1992, Cox Fernandes 1997). Neotropical stream fishes appear to be influenced by the abiotic factors of stream width (Angermeier & Karr 1983), sunlight (Power 1983), conductivity (Almirón et al. 2000), habitat diversity (Gorman & Karr 1978, Mérigoux et al. 1998) and the biotic factors of predation (Power 1984), herbivory (Wootton & Oemke 1992) and competition (Zaret & Rand 1971).

Ichthyological studies within the Ecuadorian Amazon have described the habitat and food preferences of fishes of the upper Rio Aguarico (Saul 1975). Dry season sampling has documented the Napo River drainage diversity (Stewart et al. 1987) as well as fish community patterns for riverine sandy beaches (Ibarra & Stewart 1989), lagoon and associated tributaries (Galacatos et al. 1996) and deep river and adjacent sandy beach habitats (Stewart et al. 2002).

Many of the above mentioned studies indicate highly variable stochastic fish communities (Lowe-McConnell 1987, Goulding et al. 1988, Jepsen 1997, Saint-Paul et al. 2000). However, most of these studies have limited temporal and geographic scales. As temperate studies of community structure have demonstrated, conclusions drawn from studies with extended temporal and geographic scales can differ significantly from conclusions drawn from short term and localized studies (Jackson & Harvey 1989, Strange et al. 1992, Keast 1996, Angermeier & Winston 1998, Gehrke & Harris 2000). Indeed, recent studies within the Venezuelan llanos with expanded spatial (Rodríguez & Lewis 1994, 1997) and temporal scale (Winemiller 1996) indicate that fish communities may be nonrandom, with both deterministic and stochastic processes operating.

In particular, Rodríguez & Lewis (1997) proposed the piscivore–transparency–morphometry (PTM) model for predicting floodplain lake fish assemblage patterns. The PTM model predicts that lake water transparency can largely determine the presence of major taxa and piscivore types. For example, during the dry season as water transparency decreases, the number of visually-oriented fishes, such as characiforms, cichlids and clupeomorphs, should decrease relative to nocturnal and sensory adapted piscivores, such as catfishes and knifefishes. Tejerina-Garro et al. (1998) further proposed that the PTM model also may apply to the fish communities of the Vinces River flooplain in western Ecuador.

The present study examines the seasonal occurrence of fish species within and among lagoon, river and forest stream habitats in the lower Yasuni River basin, Yasuni National Park, eastern Ecuador. We tested the following hypotheses: (1) lagoon, river and forest stream habitats have distinct fish communities; (2) fish communities within each habitat are influenced by rainfall seasonality; and (3) the PTM model (Rodríguez & Lewis 1997) will predict the dry season lagoon fish community.

Study sites

We conducted this study in the Yasuni National Reserve (Figure 1), which comprises 982 000 ha and is the largest nature preserve in Ecuador. We collected fishes from four sites representative of three habitat types: lagoon, river and stream. Site one, Jatuncocha Lagoon (0°59′46.2″S, 75°26′59.8″W), is a large shallow blackwater lagoon connected to the Yasuni River via the blackwater Jatuncocha River. Site two, Yasuni River (0°59′37.9″S, 75°25′59.1″W), is a major tributary of the Napo River that varies seasonally between conditions close to blackwater and those approaching whitewater. Sites three and four, Cotoyacu (1°00′34.7″S, 75°26′15.1″W) and Tambococha (0°58′32.6″S, 75°25′29.5″W), are groundwater-fed forest streams. Cotoyacu drains into the Yasuni River, while Tambococha drains into the blackwater Tambococha River. Jatuncocha Lagoon and Streams Cotoyacu and Tambococha are flooded blackwater habitats during the wet season.

Rainfall data collected over 13 years by the Instituto Nacional de Meteorologia e Hidrologia at Nuevo Rocafuerte reveals a dry season between December and February, and a wet season between May and June,

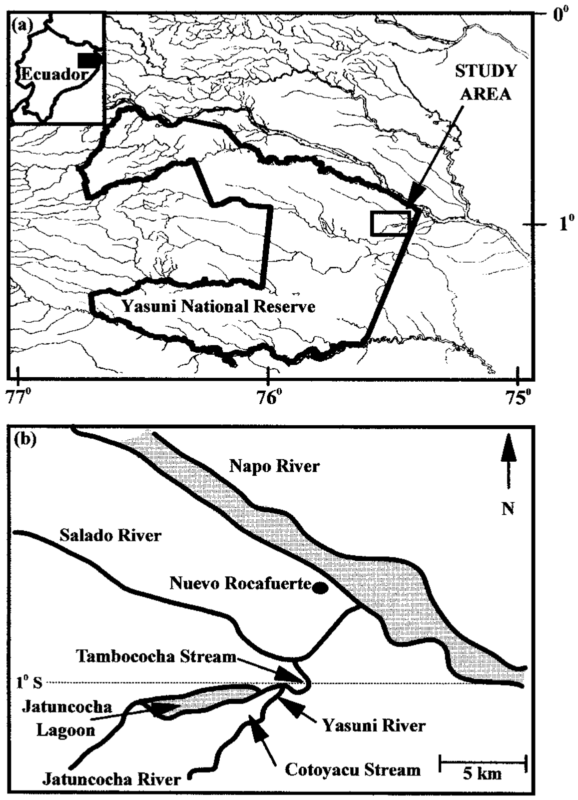

Figure 1. Study area in the Ecuadorian Amazon shown as (a) area within the Yasuni National Reserve of the Ecuadorian Amazon and (b) as schematic of study sites.

with intervening rising water and falling water seasons (Figure 2). Rainfall is highly variable (Figures 2 and 3) with the greatest relative monthly variation occurring during the dry season (Figure 3). Rainfall variability affects both the onset and duration of the wet and dry seasons.

In addition, unpredictable and heavy rainfall in local and upland regions results in rapid fluctuations in water chemistry, velocity and depth. For example, following heavy upland rainfall, the consequent heavy discharge may overwhelm the Napo and Yasuni river channels and cause whitewater to back flow into blackwater habitats like Jatuncocha Lagoon. Conversely, localized rainfall may increase blackwater discharges into whitewater habitats. Accordingly, blackwater and whitewater habitats not only occur within close proximity, but also may mix their flows at variable junctures. Unlike the predictable monomodal flood pulse and large flood amplitude associated with larger rivers and floodplains, the lower Yasuni experiences unpredictable, polymodal flood pulses associated with rainfall in headwater regions.

Materials and methods

Sampling

We sampled during four periods: rising water, February 1996; wet season, June 1996; falling water season, November 1996; and dry season, February 1997 (Figure 2). We used two gill nets in the lagoon and river and one gill net for each stream site. We used six baited minnow traps in each site. We set gill nets and minnow traps at dusk (17:00–18:00 h) each evening and fishes were collected at dawn (05:00–06:00 h). Gill nets were 1.83 m high with six 7.62 m long panels of 25.4, 50.6, 63.5, 76.2, 88.9 and 101.6 mm stretch mesh sizes, and were weighted to fish along the bottom. In addition, we set six baited minnow traps at each site. We preserved fishes in 10% formalin in the field, transferred them to 70% ethanol and deposited them in the Museo de la Escuela Politécnica Nacional (MEPN) in Quito, Ecuador.

Environmental variables

We took five measurements of temperature, dissolved oxygen, pH, turbidity and conductivity in all sites (Solomat 520c multifunctional chemistry and water quality monitor) for three seasons: rising water, wet and dry seasons. We used MANOVA (Statistica, version 5.1, StatSoft, Inc. 1998) to test the significance of seasonality and water chemistry variables within the lagoon, river and stream habitats.

Community analyses

We calculated species accumulation curves for all samples with BioDiversity Professional Program (McAleece et al. 1997) to assess effectiveness of sampling species richness within the study area. We estimated species dominance and richness within each study site by Simpson's Diversity Index, evenness and rarefaction. Simpson's Diversity Index (Simpson 1949) measures the probability that two randomly drawn individuals from an infinitely large community belong to different species. Simpson's Diversity Index is a widely used dominance measure, weighted towards the abundance of the commonest species and with low

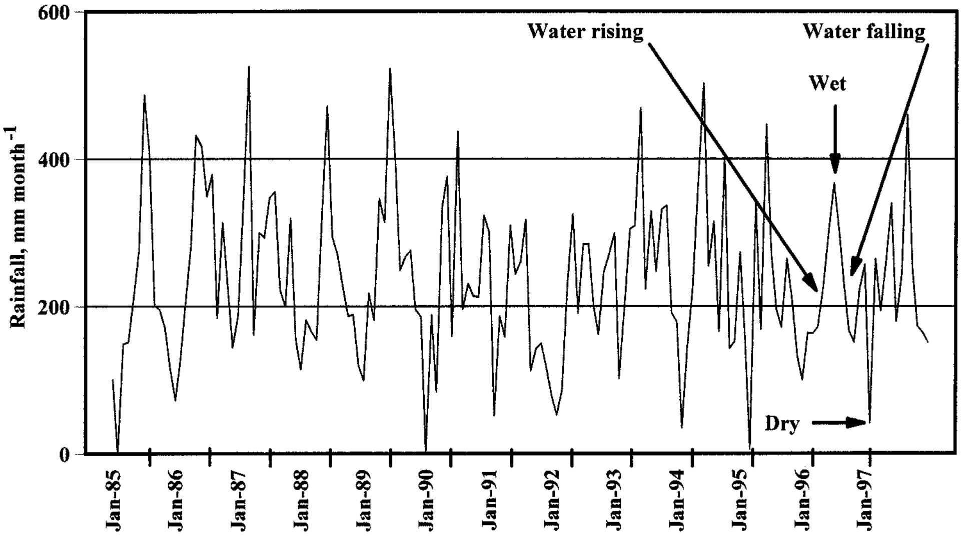

Figure 2. Total monthly rainfall (mm) December 1984 through December 1997, measured at Nuevo Rocafuerte. Sampling periods: rising water season, February 1996; wet season, June 1996; falling water season, November 1996 and dry season, February 1997.

sensitivity to sample size (Magurran 1988). We calculated evenness as the proportional abundance of each species to the total site diversity (Hill 1973). Rarefaction enables the comparison of richness in terms of expected number of species per sample among samples with different numbers of individuals. This method was proposed by Sanders (1968) and corrected by Hurlbert (1971) and Simberloff (1972). We calculated the expected number of species per sample using the EcoSim program (Gotelli & Entsminger 2001) with sample size standardized to the smallest sample size.

We used multivariate analyses of non-metric multidimensional scaling ordination (NMS) and Bray–Curtis hierarchical clustering to compare species composition among habitats, β diversity and seasons. We used PC-ORD version 4 for all three analyses (McCune & Mefford 1999). Species abundances were $\log_{10}(x + 1)$ transformed to reduce the influence of nonnormal data. We standardized water chemistry variables to zero mean and unit variance to compare variables with different scales (Jongman et al. 1995). In addition, we used NMS to examine the correlation between species composition and water chemistry variables among samples for the rising water, wet and dry seasons.

Non-metric multidimensional scaling is an ordination technique based on ranking similarities between samples. The resulting ordination reflects the relative similarity of species composition, among samples (Clarke 1993). Monotonicity, NMS's only assumption, is the linear relationship between original sample distance and first ordination axis distances. Unlike ordination techniques based on gradient analysis, such as detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA), NMS does not assume model or linear responses of either species or environmental variables. Therefore, NMS can be used with large, highly skewed species matrices typical of high diversity systems (Clarke 1993). In addition because no linear response is assumed, NMS also performs well in assessing community change with repeated samples within small geographic scales. To verify NMS ordination groupings we paired NMS ordinations with Bray–Curtis clustering using weighted group averaging (UPGMA) to link groups and Sorenson's percent similarity to scale the dendrogram (Clarke 1993).

Results

Environmental variables

Seasonality of temperature, dissolved oxygen, pH, conductivity and turbidity (Table 1) were significantly different among the study sites (df = 3, F = 2.83,

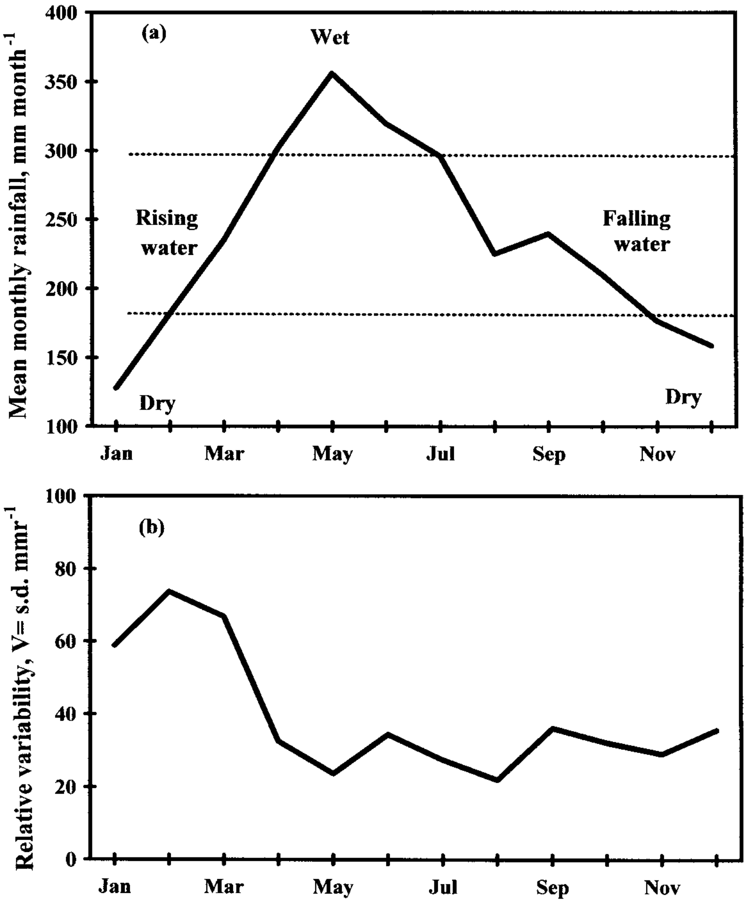

Figure 3. Monthly rainfall recorded at Nuevo Rocafuerte, December 1984 through December 1997 shown as (a) mean monthly rainfall (mm) and (b) relative variability in monthly rainfall, V, calculated from December 1984 through December 1997, where sd = standard deviation in monthly rainfall and mmr = mean monthly rainfall in mm (Hayward & Oguntoyinbo 1987).

$p = 0.047$). The blackwater lagoon had higher water temperatures, lower pH and lower conductivity than the Yasuni River and forest streams throughout all three seasons. In the lagoon, turbidity was low during the wet season, intermediate during the rising water season, and high during the dry season. River temperature and turbidity rose during the dry season, while dissolved oxygen and pH rose during the wet season. Similar seasonal changes in water chemistry occurred in streams Cotoyacu and Tambococha. During the wet season, the streams were blackwater habitats expanding into the forest with lower temperature and conductivity and higher dissolved oxygen and pH compared to rising water, falling water and dry seasons. During the dry season the streams were reduced to pools with low dissolved oxygen and high turbidity.

Community analyses

We collected 4 305 individuals from 195 species and 35 families (Appendix 1). This study increased the number of species recorded for the lower Yasuni River basin from 136 to 277 species and the number of species recorded for the Napo River to 562 species. In our collections 71% of the species belonged to three families: 50% characids, 12% pimelodids and 9% curimatids. The rate of species accumulation per additional sample was still increasing after pooling the 16 samples from all sites (Figure 4). Abundance, species richness, rarefied species richness, diversity, evenness and the percent of species and individuals varied among habitats and seasonally within each site (Figures 5 and 6).

Table 1. Mean and standard deviation for water chemistry variables measured during rising water, wet and dry seasons within lagoon, river and stream sites.

Study site	Temperature (°C)	D.O. ($\mathrm{mg\,l^{-1}}$)	pH	Conductivity ($\mu\mathrm{S\,cm^{-1}}$)	Turbidity (NTU)
Jatuncocha Lagoon					
Rising water	28.6 ± 0.6	7.7 ± 0.1	4.7 ± 0.1	10.1 ± 0.2	48.3 ± 2.7
Wet	27.8 ± 1.1	7.6 ± 0.1	4.7 ± 0.1	10.5 ± 0.6	18.1 ± 3.0
Dry	27.7 ± 0.2	8.8 ± 0.8	5.5 ± 0.2	14.7 ± 0.1	77.2 ± 0.9
Yasuni River					
Rising water	25.1 ± 0.6	7.6 ± 0.2	5.7 ± 0.1	19.6 ± 0.9	23.1 ± 3.3
Wet	25.3 ± 0.3	8.6 ± 0.5	6.8 ± 0.1	18.8 ± 0.4	20.7 ± 4.6
Dry	26.5 ± 0.2	6.8 ± 0.1	5.7 ± 0.1	20.5 ± 1.5	47.0 ± 2.6
Cotoyacu Stream					
Rising water	25.8 ± 0.3	7.5 ± 1.0	6.0 ± 0.2	27.6 ± 1.5	32.6 ± 6.3
Wet	24.7 ± 0.4	10.9 ± 0.2	6.2 ± 0.3	20.8 ± 1.1	28.7 ± 5.7
Dry	26.6 ± 0.5	0.9 ± 0.1	6.1 ± 0.2	66.6 ± 11.6	63.9 ± 4.8
Tambococha Stream					
Rising water	25.9 ± 0.1	9.2 ± 0.8	5.5 ± 0.1	28.4 ± 0.9	12.4 ± 1.5
Wet	24.6 ± 0.3	10.9 ± 0.6	6.2 ± 0.3	20.8 ± 1.1	31.6 ± 3.9
Dry	26.2 ± 0.7	1.1 ± 0.1	5.9 ± 0.3	58.9 ± 5.4	115.6 ± 5.4

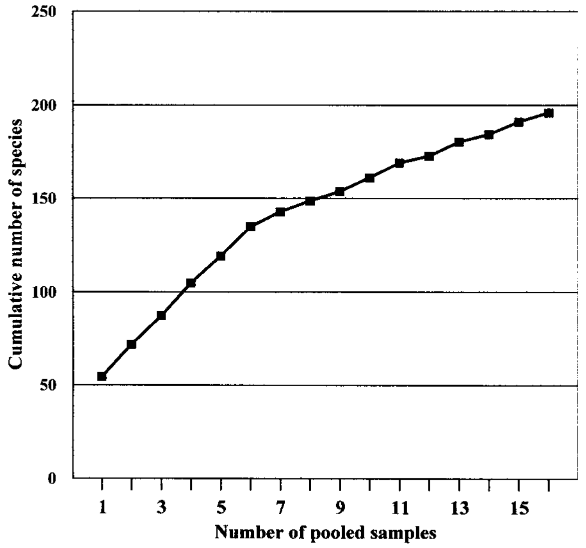

Figure 4. Cumulative number of species per each additional sample. Analysis randomly pools the samples and examines how species accumulate as samples are pooled. When asymptote is reached most of the species in a region have been collected.

Species richness was high during the dry season in both Jatuncocha Lagoon (70 species) and Yasuni River (74 species). Yasuni River diversity and evenness were lowest during the rising water sampling period and remained high for the three remaining sampling periods. In contrast, Jatuncocha Lagoon species diversity and evenness were highest in the rising water sampling period and then decreased throughout the remainder of the sampling year. Sampling within both streams was also variable. Within Cotoyacu Stream, species richness was highest during the wet season sampling period, while species diversity was constant throughout the year. Within Tambococha Stream, species richness was highest during the rising water sampling period and decreased throughout the remainder of the sampling year.

Rarefied species richness estimates were not always consistent among either habitats or seasons (Figure 5). The highest rarefied richness estimates occurred during the rising water season in the lagoon, the wet season in Cotoyacu Stream and the falling water season in the river and Tambococha Stream. The lowest rarefied species richness occurred in the falling water season for the river and in the dry season for the lagoon and streams.

Species diversity and evenness of Tambococha Stream were highest during the wet and falling water sampling periods. Rare species, single individual per species encountered, comprised 32% or 16% of the total 195 species collected. Of these, 13 were collected from Yasuni River, 6 from Jatuncocha Lagoon, 9 from Cotoyacu Stream and 4 from Tambococha Stream. In addition, the number of single specimens per sample was variable and at times comprised approximately half

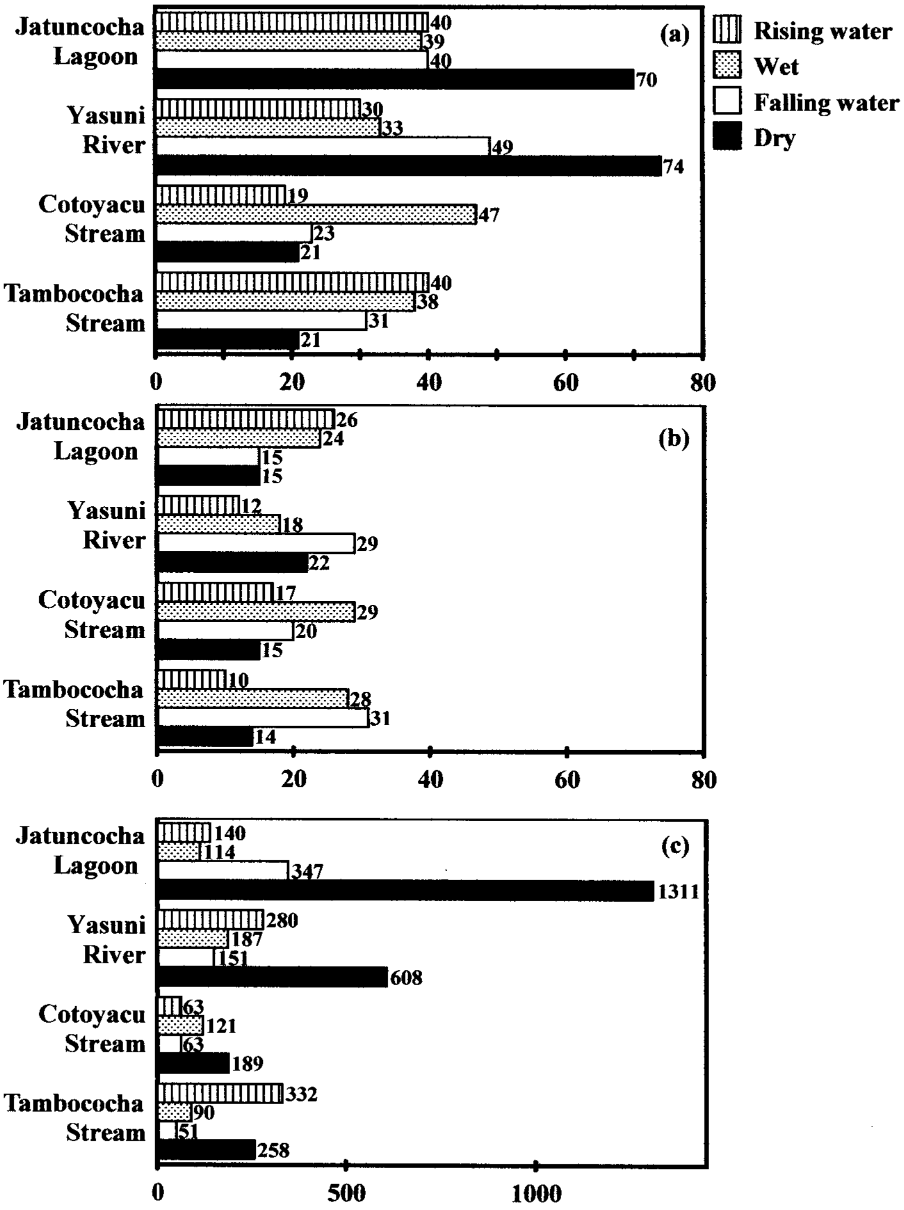

Figure 5. Seasonality of (a) number of species, (b) rarefied number of species and (c) number of individuals in various habitats of the lower Yasuni River system.

the species collected per site: 24–49% from Jatuncocha Lagoon, 32–45% from Yasuni River, 24–63% for Cotoyacu Stream and 14–63% from Tambococha Stream.

Lowland habitats can be characterized by the resident species caught throughout the sampling year (Table 2). Some of these resident species were ubiquitous, such as the piscivores *Hoplias malabaricus*, *Hydrolycus pectoralis*, *Rhaphiodon vulpinus*, *Pimelodella* sp. B and *Plagioscion squamosissimus* and the herbivore *Mylossoma duriventris*. The lagoon was further characterized by the curimatid species *Curimata vittata*, *Psectrogaster amazonica*, *Potamorhina altamazonica*, *P. latior* and

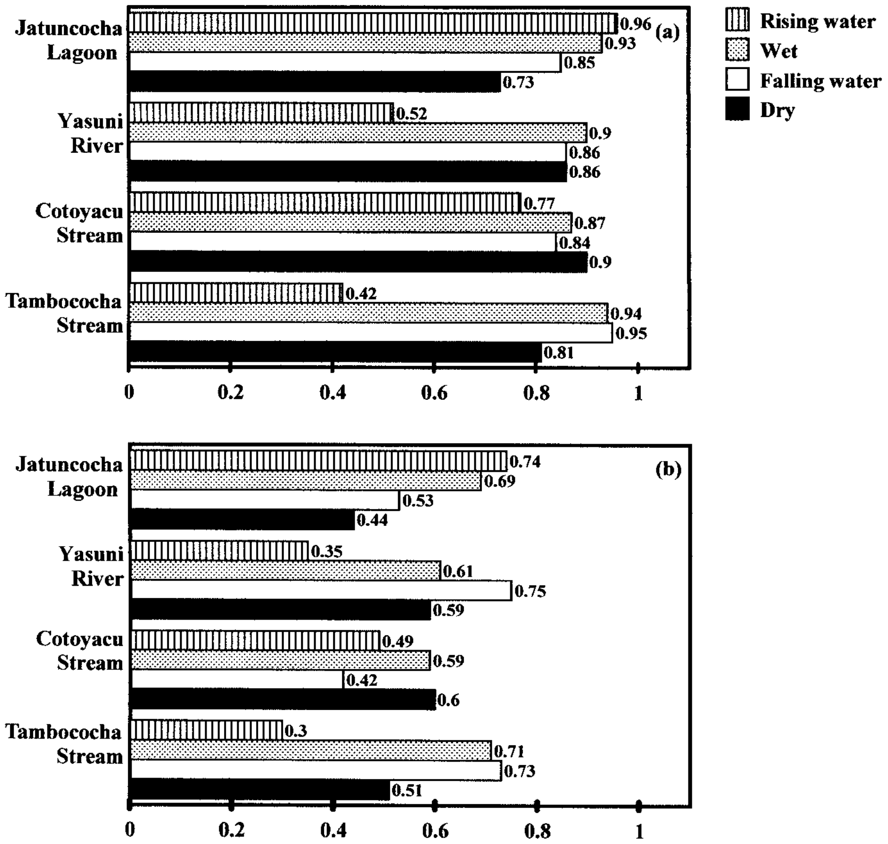

Figure 6. Seasonality of (a) Simpson's Diversity Index and (b) eveness in various habitats of the lower Yasuni River system.

Cyphocharax plumbeus. Resident species within the river included the characins *Hyphessobrycon copelandi* and *Hemigrammus* cf. *lunatus* and the catfishes *Nemadoras humeralis*, *Pimelodella* sp. G and *Sorubim* sp. A. Cotoyacu Stream's six resident species were either common lowland species or species also found in Tambococha Stream. By contrast, the 10 resident species of Tambococha Stream included *Ancistrus* cf. *alga* and *Hypselecara temporalis*, which were found only at this site.

Habitat and seasonal variation of species composition can also be examined by comparing the percent abundance of individuals within the families Characidae, Curimatidae, Doradidae, Auchenipteridae, Pimelodidae, Loricariidae and Cichlidae (Figure 7). Seasonal species composition varied not only among habitats but also seasonally within habitats.

Seasonality within the Jatuncocha Lagoon was marked by a shift in the relative abundance of characids and curimatids. Comprising from 40% to 82% of the individuals, curimatids such as *Psectrogaster amazonica*, *P. essequibensis* and *Curimata roseni* were most abundant during the rising water, wet and falling water seasons. Comprising 82% of the individuals, characids, including *Hyphessobrycon copelandi*, *Hemigrammus* cf. *lunatus*, *H. cupreus*, *H. unilineatus*, *Phenacogaster* sp. and *Poptella compressa* were most abundant during the dry season. In addition, the percent abundance of individuals for ageneiosid, auchenipterid and doradid catfishes increased during the rising water and wet seasons to 31% and 19%, respectively.

Characids and catfishes varied seasonally within Yasuni River. Characids appeared to be most numerous during the rising water season, comprising 75% of the individuals; however, this sample was dominated by the small characin *Hyphessobrycon copelandi* that comprised 68% of the individuals. Catfishes were most numerous during the wet and falling water seasons, comprising 56% and 38% of the individuals,

Table 2. Characteristic species found throughout all sampling periods within lagoon, river and stream habitats of the lower Yasuni River system.

Jatuncocha Lagoon	Yasuni River	Cotoyacu Stream	Tambococha Stream
Anodus sp. A	*Hyphessobrycon copelandi*	*Hoplerythrinus unitaeniatus*	*Hoplias malabaricus*
Hemiodus unimaculatus	*Hemigrammus* cf. *lunatus*	*Hoplias malabaricus*	*Erythrinus erythrinus*
Curimata vittata	*Phenacogaster* sp.	*Charax caudimaculatus*	*Parauchenipterus galeatus*
Cyphocharax plumbeus	*Nemadoras humeralis*	*Pimelodella* sp. B	*Ancistrus* cf. *alga*
Potamorhina altamazonica	*Ageneiosus ucayalensis*	*Sternopygus macrurus*	*Curimatella alburna*
Potamorhina latior	*Ageneiosus inermis*	*Rhamdia* sp.	*Hyphessobrycon copelandi*
Psectrogaster amazonica	*Centromochlus heckelii*		*Hypselecara temporalis*
Psectrogaster essequibensis	*Pimelodella* sp. B		*Ancanthodoras spinosissimus*
Pygocentrus nattereri	*Pimelodella* sp. C		*Gymnotus carapo*
Nemadoras humeralis	*Sorubim* sp. A		*Pimelodella* sp. B
Triportheus albus	*Hypostomus emarginatus*		
Rhaphiodon vulpinus	*Plagioscion squamosissimus*		
Plagioscion squamosissimus			

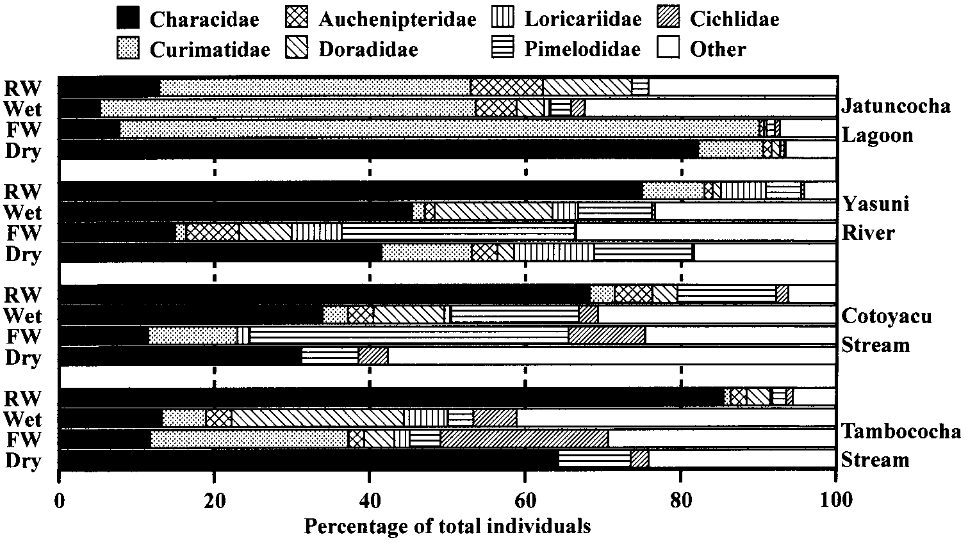

Figure 7. Seasonal variation in dominant families represented as percentage of total individuals per sample. Legend follows: RW – rising water, dry, FW – falling water and wet seasons.

respectively. Pimelodids such as *Pimelodella* sp. were most abundant during the wet (12%) and falling water (27%) seasons while the doradids, such as *Nemadoras humeralis* and *N. trimaculatus*, were most abundant during the wet season (20%). Loricariid abundance was highest (17%) during the falling water season.

Seasonality in Cotoyacu and Tambococha Streams was primarily characterized by shifts in the abundance of characids. During the rising water season, characids such as *Hyphessobrycon copelandi*, were most abundant in both streams, comprising 68% of the individuals in Cotoyacu and 86% in Tambococha. Characids were least abundant during the falling water season, comprising only 12% of the individuals in both streams. Curimatids were most abundant during the falling water season in Cotoyacu (12%) and Tambococha (26%) and entirely absent during the dry season. Callichthyids and doradids were most abundant during the wet season in Tambococha, comprising 21% and 22%, respectively. While in Cotoyacu, pimelodid relative abundance rose to the highest level, 41%, during the falling water season. Cichlid abundance was highest in the falling water season sample for

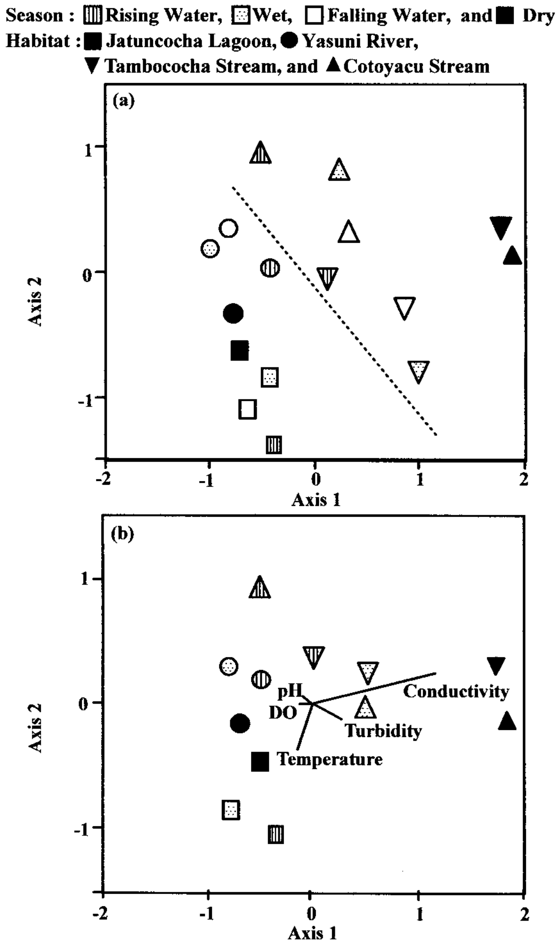

Figure 8. (a) Non-metric multidimensional scaling ordination of all 16 fish community samples. Samples grouped along axis 1 primarily by habitat type. The dashed line separates the stream samples from the lagoon and river samples. (b) Non-metric multidimensional scaling ordination of 12 fish community samples with biplot of water chemistry variables of temperature, turbidity, conductivity, pH and dissolved oxygen (DO).

both streams, with 10% in Cotoyacu and 22% in Tambococha.

We performed NMS first, on all 16 samples collected from the lagoon, river and two stream sites and, second, on the 12 samples with corresponding water chemistry variables from the rising water, wet and dry seasons (Figure 8). Both NMS ordinations had monotonocity, with high cumulative coefficients between ordination distances and the distances in the original n-dimensional space: NMS ordination of 16 samples had a cumulative $r^2 = 0.82$ ($r^2 = 0.53$ for axis-1 and 0.21 for axis-2); and NMS ordination of 12 samples with water chemistry variables had a cumulative $r^2 = 0.86$ ($r^2 = 0.56$ for axis-1 and 0.30 for axis-2).

The NMS ordination and Bray–Curtis clustering of the 16 sites resulted in similar groupings, based primarily on habitat and secondarily on season (Figures 8 and 9). Within the ordination, the dry season samples were the most distinct group, followed by the rising water, wet and falling water season stream samples. The rising water, wet and falling water season river samples grouped together. The dry season river sample grouped between the other river samples and the lagoon samples. Within the Bray–Curtis dendrogram the overall similarity among groups was low. The dry season stream group, forming the first branch of the dendrogram, had 9% similarity to all other samples. The second branching within the dendrogram contained the falling water and wet season stream

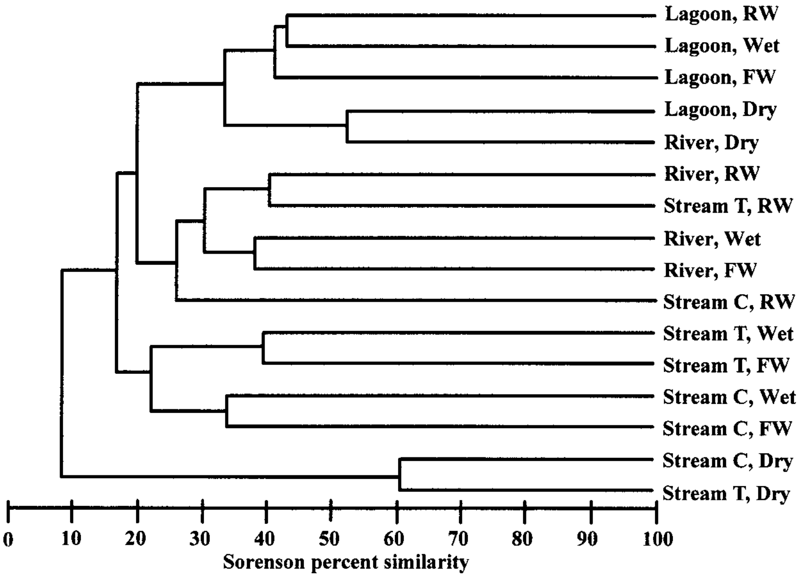

Figure 9. Bray–Curtis hierarchical clustering of all 16 fish community samples. Dendrogram scaled with Sorenson percent similarity. Legend follows: Lagoon – Jatuncocha, River – Yasuni, Stream T – Tambococha Stream, Stream C – Cotoyacu Stream, RW – rising water, wet, FW – falling water and dry seasons.

samples and had 18% similarity to the remaining rising water stream, river and lagoon samples. The third dendrogram branch had 21% similarity and separated the group consisting of the rising water season stream samples and the rising water, wet and falling water season river samples from the group consisting of the lagoon and dry season river samples. The fourth branch with 27% similarity separated the rising water season Cotoyacu Stream sample from the rising water, wet and falling water season river samples.

The dry season lagoon and river grouping was comprised of a large number (40) of shared species. For example, the characins *Hyphessobrycon copelandi*, *Hemigrammus* cf. *lunatus*, *Phenacogaster* sp. and *Triportheus angulatus* and the piscivore *Ageneiosus inermis* were very abundant in both lagoon and river dry season samples. In addition, the curimatids, *Curimata vittata*, *Cyphocharax laticlavius*, *C. plumbeus*, *C. spiluropsis*, *Potamorhina latior* and *P. altamazonica* were found year long within the lagoon and in the dry season river sample.

The highest within group similarity occurred for the dry season stream samples (60%) and the dry season lagoon and river samples (52%). Moderate to low similarity occurred between the falling water and wet season sample pairs for Cotoyacu Stream (33%), Tambococha Stream (39%) and Yasuni River (38%). The rising water Tambococha Stream and Yasuni River had 41% similarity. The rising water, wet and falling water season lagoon samples had 42% similarity.

The NMS ordination of the rising water, wet and dry season samples with water chemistry variables revealed similar groupings with the NMS of all 16 samples and the correlation of habitat and water chemistry variables (Figure 8). High conductivity was associated with the desiccating pools of the dry season stream samples. Higher dissolved oxygen and pH were associated with all Yasuni River samples and the rising water stream samples. Jatuncocha Lagoon had high temperatures throughout the three seasons.

Piscivore–Transparency–Morphometry (PTM) model

To test the PTM model, we calculated the percent abundances of characiform and siluriform individuals within Jatuncocha Lagoon. The dry season sampling occurred at the end of the dry season, when water levels within the Jatuncocha Lagoon were lowest and turbidity highest (Table 1). The siluriforms were abundant during both the wet and dry season, while the characiforms were most abundant during the falling water and dry seasons. Furthermore, the characiform piscivores *Pygocentrus nattereri* and *Rhaphiodon vulpinus* were common, characteristic lagoon species encountered during all seasons.

Discussion

Environmental variables

Seasonal changes in environmental variables reflected the wet season expansion and dry season contraction of lagoon and stream habitats. However, the changes within the Yasuni River may have been, in part, influenced by water inputs from other habitats. For example, the temperature and turbidity increases noted for the Yasuni River during the dry season, may have been influenced by the inflow of the blackwater Jatuncocha River. During the wet season, the Yasuni River had higher dissolved oxygen and pH than other habitats. This may have been attributable to headwater discharges that gave the river transient whitewater features.

Community analyses

Seasonal sampling yielded highly variable species richness and abundances within the lagoon, river and stream habitats. All study sites had a mix of resident, characteristic species (Table 2) and seasonal species (Figure 7). Dry season sampling in the river and lagoon habitats netted the highest number of species and individuals, as has been reported for other Amazonian lakes (Saint-Paul et al. 2000, Silvano et al. 2000) and rivers (Goulding et al. 1988). In contrast, the highest species richness was found either during the rising or wet seasons for the stream habitats.

No one season yielded the highest rarefaction richness estimates among all habitats. These rarefaction results differ from those of the upper Juruá River in Brazil where Silvano et al. (2000) found higher rarefied estimates during the dry season for lake, river and tributary habitats. However, Silvano et al. (2000) combined samples from different locations and the number of samples varied for each habitat type between seasons.

The grouping of the rising water samples for Tambococha Stream and Yasuni River is explained in part by the high abundances of *Hyphessobrycon copelandi* and by the 13 shared species like *Hemigrammus* cf. *lunatus* and *Nemadoras humeralis*. In contrast, the rising water Cotoyacu Stream sample clusters alone in part due to the low abundance of *H. copelandi* and the absences of *Hyphessobrycon* cf. *bentosi* and *N. humeralis*.

The grouping of wet and falling water season samples within the river and stream samples can be explained by the abundance of a few shared species. For example *Pimelodella* sp. B and *Sternopygus macrurus* characterize the grouping of the falling water and wet season Cotoyacu samples, while *Hoplosternum littorale* and *Ancistrus* cf. *alga* characterize the grouping for the wet and falling water season Tambococha samples. *Nemadoras trimaculatus*, *Pimelodella* sp. K and *Loricaria* sp. characterize the wet and falling water season river samples.

The large variability in fish among and within habitats may have been due to sampling methodology and the region's high species richness (Stewart et al. 1987, Galacatos et al. 1996). It is possible that increased numbers of gill nets, minnow traps and sampling days could lower the variability and decrease the rate of new species encountered per additional sample. However, if diel and microhabitat sampling were incorporated, the addition of diurnal and habitat-specific species would probably increase sample variability. While only 16% of the species of the study's 195 species were rare species (one individual per species), the number of single individuals per sample was high, up to 49% for Jatuncocha Lagoon, 45% for the Yasuni River, 63% for Cotoyacu Stream and 65% for Tambococha Stream. However, even with the limited sampling methodology, seasonal sampling augmented the number of fish species recorded for the lower Yasuni now (277 species) and for the Napo River Drainage (562 species). Furthermore, the steady increase in species accumulation (Figure 4) indicates that the fish fauna of the lower Yasuni remains under sampled.

Seasonal variation within lagoon, river and stream sites reflected species-specific responses to changing environmental conditions, feeding and reproductive migrations. Junk et al. (1989) and Cox Fernandes (1997) have shown a correlation between fish migrations and changes in oxygen. For example, pimelodids migrate upriver to feed during the dry season (Goulding 1980, Lowe-McConnell 1987, Barthem & Goulding 1997). However, the pimelodids *Brachyplatystoma vaillantii*, *Hemisorubim platyrhynchos*, *Platynematichthys notatus*, *Platystomatichthys sturio* and *Sorubim lima* were found during both falling water and dry seasons, which suggests that within the lower Yasuni these species may begin migrating earlier than the dry season. While studies have noted seasonal variability in fish communities between dry and wet season, the results of this study and Saint-Paul et al. (2000) demonstrate the seasonal variability between rising and falling water seasons.

Piscivore–Transparency–Morphometry (PTM) model

Seasonal sampling within Jatuncocha Lagoon allowed us to test the PTM model proposed by Rodríguez & Lewis (1997) for the Orinoco floodplain lakes and tested within the Amazonian floodplain lakes of the Araguaia River, Brazil (Tejerina-Garro et al. 1998). The PTM model predicts that as water transparency and water depth decrease the relative abundance of diurnal, vision-oriented fishes like characiforms should decrease relative to nocturnal or to low light fishes like siluriforms. Thus, according to the PTM model, at the end of the dry season, the lagoon should have a relatively lower percentage of characiform fishes and a higher percentage of siluriform fishes. However, within Jatuncocha Lagoon, siluriforms were abundant during both the wet and dry seasons, while the characiforms were most abundant during the falling water and dry seasons.

These results do not appear to support the PTM model and contrast with those of Rodríguez & Lewis (1997) and Tejerina-Garro et al. (1998). Sampling methodology may partially explain this contrast. Rodríguez & Lewis (1997) and Tejerina-Garro et al. (1998) used Secchi disc readings to measure transparency and turbidity while our study measured only turbidity. Our sampling methodology concentrated on seasonality and increased sampling effort (12 consecutive days) during each sampling period within a few sites. In contrast, Rodríguez & Lewis (1997) sampled 20 lakes using electrofishing and Tejerina-Garro et al. (1998) sampled 12 lakes using gill nets. For both of those studies, samples were taken at the beginning and end of the dry season. Their sampling methodology, thus, concentrated on increasing the number of sampled lakes with reduced sampling effort per lake (1 or 2 consecutive days). Differences in the time of sampling could have influenced differences in results. Our sampling period occurred between dusk and dawn, while the sampling periods for both Rodríguez & Lewis (1997) and Tejerina-Garro et al. (1998) occurred during the day and were biased against nocturnal catfish. The PTM model addresses fish community patterns only during the dry season within large floodplain lakes. Therefore, the PTM model may not be applicable to the blackwater Jatuncocha Lagoon, which experiences polymodal floodpulses typical of smaller headwater regions and is not isolated during the dry season.

Conservation and management considerations

The lagoon, river and stream habitats of the lower Yasuni were characterized by seasonally dynamic water chemistry, high species diversity and turnover among habitats. The high seasonal variability of these parameters suggests that studies of Amazonian fish communities should include seasonal sampling. Management and assessment of environmental impacts may be difficult in communities where the contribution of rare species is high (Grossman et al. 1990).

The Ecuadorian Amazon, like many other regions within the Amazon basin, is being impacted by human settlement, deforestation and oil production. Such activities affect the aquatic environment that provides not only local water and food resources (Kimberling 1993, Hettler et al. 1996) but also feeding and spawning habitats for migratory species. Furthermore, the presence of migratory pimelodid species within the lower Yasuni supports Barthem & Goulding's (1997) recommendation that Ecuador be included in the conservation and management of Amazonian catfishes. Studies have already assessed the over-exploitation of Amazonian fisheries (Bayley & Petrere 1989, Welcomme 1990), however, studies are needed to identify and then assess the status of critical spawning and feeding habitats.

Acknowledgements

This study was supported by a Fulbright Fellowship to Katerina Galacatos as part of doctoral research. The State University of New York, College of Environmental Science and Forestry, Escuela Politécnica Nacional and the Instituto Ecuatoriano Forestal y de Areas Naturales y Vida Silvestre (INEFAN) generously provided laboratory, logistical and field assistance. The Instituto Nacional de Meteorologia e Hidrologia provided access to rainfall data. This study was also facilitated, in part, by a grant to D. Stewart and R. Barriga from the National Geographic Society. Specimens were collected under permit #003-IC INEFAN DANVS/VS to Katerina Galacatos. A.S. Flecker, M. Ibarra, N. Ringler, M.A. Rodríguez and two anonymous reviewers provided essential input and critical commentary.

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Appendix 1. Species by sample matrix. Sites ordered by ordination and classification results. T – Tambococha Stream; C – Cotoyacu Stream; Y – Yasuni River; J – Jatuncocha Lagoon; R – Rising water season; W – Wet season; F – Falling water season; and D – Dry season.

No.	Species	T D	C D	C R	C W	C F	T R	T W	T F	Y R	Y W	Y F	Y D	J D	J R	J F	J W
1	*Potamotrygon motoro*													2			1
2	*Potamotrygon* sp. A													2			2
3	*Osteoglossum bicirrhosum*													4			1
4	*Pristigaster whiteheadi*												5				
5	*Pellona castelnaeanus*												2			1	3
6	*Illisha amazonica*									1		2					
7	*Lycengraulis batesii*											2					
8	*Hoplias malabaricus*	3	7		4	5	1	3	2				1	5		3	
9	*Erythrinus erythrinus*	6	12				2	4	5								1
10	*Hoplerythrinus unitaeniatus*		1		1	1		2									
11	*Boulengerella maculata*												1	1		2	
12	*Boulengerella cuvieri*											3					
13	*Copeina guttata*	12	13														
14	*Pyrrhulina* sp. A	10	37														
15	*Pyrrhulina* sp. B	4	5														
16	*Pyrrhulina* sp. C	2															
17	*Anodus* sp. A					2						3	5	2	6	2	4
18	*Hemiodus unimaculatus*												3	4	1	2	3
19	*Caenotropus labyrinthicus*						3										
20	*Chilodus punctatus*													1			

Appendix 1. (*Continued*)

No.	Species	T D	C D	C R	C W	C F	T R	T W	T F	Y R	Y W	Y F	Y D	J D	J R	J F	J W
21	*Laemolyta garmani*														3	1	
22	*Leporinus agassizi*“‘																1
23	*Leporinus* cf. *muyscorum*			1			1		1								
24	*Leporinus niceforoi*					1						1	2		1		
25	*Leporinus trifasciatus*						1										
26	*Rhytiodus microlepis*											2				1	
27	*Schizodon fasciatus*						1		1			3					
28	*Prochilodus nigricans*													5			
29	*Curimata vittata*												1	14	11	35	8
30	*Curimata cisandina*									1	2					1	
31	*Curimata roseni*								3	4	1		2		4	13	
32	*Curimata aspera*								2						1	6	1
33	*Curimatopsis macrolepis*													23			
34	*Curimatella alburna*						1	2	2	1						1	
35	*Curimatella meyeri*			1		1		1	3	1			11			65	
36	*Cyphocharax laticlavius*												1	3			
37	*Cyphocharax notatus*			1		1	1		1						1		4
38	*Cyphocharax plumbeus*												2	18	9	1	3
39	*Cyphocharax spiluropsis*												3	17		1	
40	*Potamorhina latior*												4	12	1	2	5
41	*Potamorhina altamazonica*												1	3	4	4	15
42	*Psectrogaster amazonica*						1	1		14	1		8	8	12	23	19
43	*Psectrogaster essequibensis*							1	2					4	6	101	
44	*Psectrogaster rutiloides*														7		
45	*Steindachnerina bimaculata*				3	5				1		2	16	8		33	
46	Curimatid undet.				1												
47	*Thoracocharax stellatus*					2						1					
48	*Thoracocharax securis*					1											
49	*Carnegiella schereri*				7												
50	*Carnegiella strigata*		1					1									
51	*Cynodon gibbus*														2		
52	*Hydrolycus scomberoides*						1			6		2	8	5		1	2
53	*Rhaphiodon vulpinus*				1						1	3	3	4	3	2	1
54	*Acestrocephalus boehlkei*											1					
55	*Acestrorhynchus abbreviatus*								2				2	2	1	2	
56	*Acestrorhynchus falcirostris*													2	1		
57	*Acestrorhynchus microlepis*												1	4			
58	*Aphyocharax* sp.									1							
59	*Astyanax* cf. *fasciatus*										1						
60	*Bryconella pallidifrons*	20															
61	*Characidium* sp. I		16														
62	*Cynopotamus amazonus*				1												
63	*Charax caudimaculatus*			3	1	4								2			
64	*Colossoma macropomum*												2				
65	*Ctenobrycon hauxwellianus*											1	1				
66	*Hemigrammus cupreus*													12			
67	*Hemigrammus* cf. *lunatus*			3	4		4			8	2	7	208	286		1	
68	*Hemigrammus luelingi*	3	10														
69	*Hemigrammus ocellifer*	19												1			
70	*Hemigrammus unilineatus*				6		5			1			3	12			
71	*Holoshestes* sp.												3	7			
72	*Hyphessobrycon* cf. *bentosi*	3					18			4				25			
73	*Hyphessobrycon copelandi*	6		28	5		253	1		192	25	1	57	612			

Appendix 1. (*Continued*)

No.	Species	T	C	C	C	C	T	T	T	Y	Y	Y	Y	J	J	J	J
		D	D	R	W	F	R	W	F	R	W	F	D	D	R	F	W
74	*Hyphessobrycon* cf. *heterorhabdus*	101	29		10			3						1			
75	*Hyphessobrycon* cf. *serpae*										7						
76	*Hyphessobrycon* sp.	1								1							
77	*Hyphessobrycon* cf. *tukunai*	13	3														
78	*Knodus* cf. *beta*										5						
79	*Moenkhausia cotinho*				2												
80	*Moenkhausia dichroura*				2			1			1			7			
81	cf. *Moenkhausia,* undet. juv.				2												
82	*Myleus* sp. A													2			
83	*Myleus* cf. *rubripinnis*														1		
84	*Metynnis* sp. A		1														
85	*Mylossoma aureum*													1	1		
86	*Mylossoma duriventris*			1				1	1			4	2	14			
87	*Phenacogaster* sp.			6		1	1				8	1	33	18			
88	*Piaractus brachypomus*												1				
89	*Poptella compressa*				1									34			
90	*Pygocentrus nattereri*													6	1	9	1
91	*Roeboides myersii*				1		1	2				1	8				
92	*Salminus* cf. *hilarii*											1	1				
93	*Serrasalmus elongatus*													1			
94	*Serrasalmus rhombeus*						1	1		2	1	1	3	7		4	1
95	*Serrasalmus* sp. A							1			1			1			
96	*Stethaprion erythrops*					1							1				
97	*Tetragonopterus argenteus*								1			2					
98	*Tetragonopterus chalceus*				1		1		1		1		1				1
99	*Triportheus albus*			1	1								1	3	2	1	1
100	*Triportheus angulatus*				2	1		1					12	12	7	1	
101	*Triportheus elongatus*							1	1	1	2		18	4	4	9	2
102	*Triportheus culter*												2				
103	*Triportheus pictus*			1													
104	*Tyttobrycon* sp.				2												
105	*Acanthodoras spinosissimus*				1		2	1	1						1		
106	*Agamyxis pectinifrons*				3			1									
107	*Amblydoras affinis*				1		1		1				1	2			
108	*Anadoras grypus*													2	5		
109	*Doras punctatus*				1			2									
110	*Nemadoras humeralis*				4		6	7		3	15	6	8	6	7	1	3
111	*Nemadoras elongatus*													2	1		1
112	*Nemadoras trimaculatus*			2				5			21	3					
113	*Nemadoras* cf. *trimaculatus*							4			1						
114	*Oxydoras niger*														2		
115	*Physopyxis* sp.													1			
116	*Platydoras costatus*				1		1										
117	*Ageneiosus vittatus*												1				
118	*Ageneiosus ucayalensis*				2						1	6	3	3			
119	*Ageneiosus inermis*				2	1				2	2	4	15	17	1		
120	*Ageneiosus* sp. D			1	4		1						3	2	11		4
121	*Auchenipterichthys thoracatus*			1			2					1	2		3		
122	*Auchenipterus ambyiacus*											1	2	3	4		3
123	*Centromochlus heckelii*						1				3	5	2	4			2
124	*Centromochlus* sp.											1			3		1
125	*Trachelylopterus galeatus*				4		3	3	1	3		1	7	6	3	2	
126	*Tatia intermedia*			2			1						1	2			

Appendix 1. (*Continued*)

No.	Species	T	C	C	C	C	T	T	T	Y	Y	Y	Y	J	J	J	J
		D	D	R	W	F	R	W	F	R	W	F	D	D	R	F	W
127	*Brachyplatystoma vaillantii*											1	1				
128	*Brachyrhamdia* cf. *marthae*					1											
129	*Calophysus macropterus*												3	2			
130	*Gladioglanis conquistidor*	24	13														
131	*Hemisorubim platyrhynchos*												4			1	
132	*Hypophthalmus* sp. A														1		1
133	*Hypophthalmus* sp. B										1						
134	*Imparfinis* sp.				1												
135	*Pimelodella* sp. C						2										
136	*Pimelodella* sp. F			7	13	18	1	1	1	3	9	19	9	4		1	
137	*Pimelodella* sp. G			1						6	3	4	15				
138	*Pimelodella* sp. H											1					
139	*Pimelodella* sp. I				1	5	2						1				
140	*Pimelodella* sp. K										9	7	11				1
141	*Pimelodina flavipinnis*														2		
142	*Pimelodus* sp. C				1							1	4			1	1
143	*Pinirampus pirinampu*									2		1					
144	*Platynematichthys notatus*												1				
145	*Platystomatichthys sturio*											3	1				
146	*Pseudopimelodus* sp.				1												
147	*Rhamdia* sp.		1		3	1		1	1				1				
148	*Sorubim lima*											2					
149	*Sorubim* sp. A						1	1		1	1	1	2			1	
150	*Sorubim elongatus*									1							
151	*Hemicetopsis candiru*				1												
152	*Bunocephalus bifidus*	15	12														
153	*Bunocephalus verrucosus*		3		1									1			
154	*Branchioica* sp.													1			3
155	*Tridentopsis* sp.	1	11														
156	*Callichthys callichthys*						1	2									
157	*Hoplosternum littorale*				1			15	2		13						
158	*Dianema longibarbis*				1		1										
159	*Megalechis thoracata*	1						2									1
160	*Ancistrus* cf. *alga*						1	4	1								
161	*Hypostomus emarginatus*									10		14	25				
162	*Hypostomus* sp.				1			1			2		2	1			
163	*Lamontichthys filamentosus*									1							
164	*Loricaria simillima*									1							
165	*Loricaria* sp.										5	2	3				
166	*Otocinclus macrospilus*											3					
167	*Peckoltia ucayalensis*					1					1	4	1				
168	*Rineloricaria* sp.																1
169	*Sturisoma guentheri*									4		3	13				
170	*Gymnotus carapo*		4				1	1	2								1
171	*Electrophorus electricus*										1						
172	*Apteronotus macrostomus*												2				
173	*Sternarchogiton* sp.												1				
174	*Rhamphichthys* sp.				2							3			2	1	
175	*Eigenmannia* cf. *limbatus*				2	1			1			2	1	2	2		
176	*Rhabdolichops troscheli*													1			
177	*Sternopygus macrurus*			1	8	3	2	6				2	6	1		2	1
178	*Steatogenys elegans*								1								
179	*Rivulus limoncochae*	8	3														
180	*Plagioscion squamosissimus*						2	1		3	39	6	12	24		6	3

Appendix 1. (*Continued*)

No.	Species	T	C	C	C	C	T	T	T	Y	Y	Y	Y	J	J	J	J
		D	D	R	W	F	R	W	F	R	W	F	D	D	R	F	W
181	*Aequidens tetramerus*	4	6						5								
182	*Aequidens* cf. *diadema*							1									
183	*Apistogramma cruzi*	2					1							1			
184	*Astronotus ocellatus*								1								
185	*Burjurquina* sp.												1				
186	*Cichla monoculus*			1													
187	*Crenicichla anthurus*				1		1		1								
188	*Crenicichla cincta*					5					1					2	2
189	*Crenicichla proteus*				2	1		2	1	1							
190	*Heros efasciatus*								1								
191	*Hypselecara temporalis*						1	2	2								
192	*Laetacara flavilabris*		1														
193	*Satanoperca jurupari*													1			
194	*Hypoclinemus mentalis*			1									4	1		1	5
195	*Colomesus asellus*														2		