Diel changeover in sandbank fish assemblages in a neotropical floodplain river

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(Received 4 October 2002, Accepted 5 June 2003)

Fishes were collected over 7 months (February to June and November to December 1999) from seven sandbanks located on the main channel of the Cinaruco River, Venezuela. Significant shifts in assemblage structure and species richness were documented between diurnal and nocturnal samples. Seine samples standardized for effort yielded 41 604 individual fishes representing seven orders, 25 families, 80 genera and 134 species. Nocturnal samples yielded 68% of the total individuals, and 54% of species were collected exclusively at night. Nocturnal samples were significantly more species rich than their paired diurnal samples, even after rarefaction. Correspondence analysis revealed consistent differences in assemblage structure between diurnal and nocturnal samples probably due to species-specific habitat use and activity patterns. In spite of the magnitude of seasonal variation in hydrology and habitat availability in the Cinaruco River, species richness and abundance on sandbanks varied relatively little. The study of biological diversity and understanding of patterns of habitat use in a neotropical river were enhanced by nocturnal sampling.

Key words: assemblage structure; diurnal; *llanos*; nocturnal; species richness; Venezuela.

INTRODUCTION

Diel variation in fish assemblage structure is well documented in temperate fresh waters (Helfman, 1981), estuaries (Robblee & Zieman, 1984; Nagelkerken *et al.*, 2000), fjords (Nash, 1986), coastal surf zones (Ross *et al.*, 1987; Layman, 2000), coral reefs (Collette & Talbot, 1972; Rooker *et al.*, 1997) and tropical mangroves (Rooker & Dennis, 1991; Laroche *et al.*, 1997). Changes in ambient light concentrations at twilight and dawn trigger changeover in assemblage structure (Helfman, 1981; Robblee & Zieman, 1984). Changes in abundance of individuals and species are often attributed to diel shifts in habitat use associated with shifts in foraging activity (Rooker & Dennis, 1991; Burrows *et al.*, 1994; Piet & Guruge, 1997) and predator avoidance (Wright, 1989; Copp & Jurajda, 1993; Burrows *et al.*, 1994; Gibson *et al.*, 1998).

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Among ecological studies of neotropical fish assemblages, few studies have characterized both diurnal and nocturnal assemblages at a single location. Lowe-McConnell's (1964) descriptions of the ecology of the fishes of the Rupununi savanna of Guyana provide insight into the 'remarkable' diel changeover that occurs in fish assemblages. Lowe-McConnell (1964) noted that nocturnally active siluriforms and gymnotiforms emerged from diurnal refuges to forage, whereas diurnally active cichlids and characids became inactive nocturnally. She speculated that nocturnal inactivity by cichlids and most characids probably helps them avoid detection by predatory catfishes, many of which have well-developed olfaction and abilities to detect turbulence from swimming organisms (Pohlmann *et al.*, 2001).

Although it is known that many neotropical fishes change activity patterns on a diel basis, diurnal and nocturnal changes in assemblage structure have not been demonstrated. Although diel variation in temperate fish assemblages has been shown, patterns appear to be system specific. For example, species richness in the surf zone is higher at night (Layman, 2000), but in estuaries species richness is greater during the daytime (Nagelkerken *et al.*, 2000). In the present study, fishes were sampled systematically from sandbank habitats in a large, neotropical floodplain river in order to quantify diel variation in species richness, number of individuals and assemblage structure.

MATERIALS AND METHODS

STUDY SITE

Samples were collected from the Cinaruco River, Apure State, Venezuela, between $6^{\circ}32'$ N; $67^{\circ}25'$ W and $6^{\circ}34'$ N; $67^{\circ}13'$ W (Winemiller *et al.*, 1997). This moderate black-water tributary of the Orinoco River is characterized by low pH, low conductivity and low suspended solids (Winemiller *et al.*, 1997). The Cinaruco River supports >260 fish species (www.neodat.org), most of which are characteristic of Amazonian blackwater rivers. The river meanders through an extensive floodplain inundated by seasonal water level changes (Fig. 1). During the low-water period (January to April), the aquatic habitat is limited to the main-channel, side channels and lagoons. Mean channel width during the dry season is *c*. 80–100 m. During May, rising water floods the gallery forest and flanking savanna and greatly increases the volume of aquatic habitat. Highest water levels are generally observed in September.

FIELD SAMPLING

Paired diurnal and nocturnal samples of fishes were collected monthly from riverchannel sandbanks in February, March, April, May, June, November and December 1999. For the purpose of this study, sandbanks are defined as point bars that form on the convex (inner) banks of river meanders. Sandbanks are gradually exposed as the water level recedes during the dry season. Seven main-channel sandbanks were sampled each month, except November (six) by seining. Sandbanks were located in the active channel, and were located along an 8 km reach c. 55 km upstream from the confluence with the Orinoco River. The same seine $(6.4 \times 1.8 \text{ m} \text{ with } 4 \text{ mm mesh})$ was used to collect all samples. Each sandbank sample was a composite of three contiguous (non-overlapping) seine hauls (10 m in length) taken parallel to the shore, which resulted in 30 m of shoreline being sampled. During seine hauls, one end of the seine was pulled along the shoreline and the other end was pulled in a parallel direction c. 4.5 m offshore. At the offshore end of the seine, average sample depth was mean \pm s.D., $44.3 \pm 21.4 \text{ cm}$ and mean water



FIG. 1. Seasonal fluctuation in Cinaruco River water levels during 1999, and corresponding temporal variation in mean \pm s.e. (a) species richness and (b) number of individuals of fishes collected in nocturnal (\square) and diurnal (\square) sandbank seine samples. • • •, water elevation. n = 7 except November when n = 6.

velocity was 0.19 ± 0.11 m s⁻¹. Diurnal samples were collected each month over a 2 day period between 0800 and 1800 hours (average time of sampling 1330 hours). Nocturnal samples were collected in a single night between 2000 and 0100 hours (average time of sampling 2200 hours) from 4 days prior to 9 days after diurnal sampling, with a median separation of 4 days between diel samples. Mean absolute difference in river height between monthly diurnal and nocturnal sampling was 15 cm (maximum 36 cm in November),

a tiny fraction of the annual hydrologic variation (c.5 m). Each month, a random number generator was used to select sampling order of sandbanks and the portion of each sandbank to be sampled. To control for potential effects of environmental variables (e.g. water depth and velocity) on assemblage structure, each nocturnal sample was collected from the same section of sandbank as the corresponding diurnal one.

Because efficiency of diurnal seining may be lower than nocturnal seining (Holland-Bartels & Dewey, 1997), diurnal castnet samples were collected to document the presence of fish species on sandbanks that evaded capture in diurnal seine samples. Monthly diurnal castnet samples were collected on the same sandbanks that were seined. Each month, c. 1–2 h after diurnal seining was completed, six to eight throws were made in the vicinity of the seined area with a monofilament castnet (2·44 m radius; 9·5 mm mesh). Throughout the study, castnet throws were made by the same individual. Six to eight throws from each sandbank were combined to form a single castnet sample for that sandbank for each month. Castnet samples were never combined with seine data, rather the two were treated as independent data sets.

For each sample, fishes were preserved in 10% formalin and later transferred to 70% ethanol. All specimens were sorted, and as many as possible were identified to species level. Similar to Stewart *et al.* (2002), undescribed taxa were designated with a generic name and letter (*e.g. Characidium* sp. A). Some small juveniles were identified to genus only (*e.g.* piranhas *Serrasalmus* spp.). Identified specimens were counted in the laboratory. Specimens were archived in natural history collections (Museo Ciencias Naturales Guanare, Guanare, Portuguesa, Venezuela and Texas Cooperative Wildlife Collection, College Station, TX, U.S.A.).

DATA ANALYSIS

Species richness, number of individuals and assemblage structure were compared between paired diurnal and nocturnal samples. Because sampling effort was standardized, species richness was first compared without controlling for the number of individuals collected. A split-plot, repeated measures ANOVA was used to test for differences in species richness and the number of individuals between paired diurnal and nocturnal samples. Between-subjects effects due to location (location of the sandbank) and diel period within a given location [Diel (Location)] were examined. Within-subjects effects due to interactions between month and location and month and diel period within a given location were also examined. Raw data were square-root transformed to meet assumptions of normality and homogeneity of variance (Zar, 1996). To control for the likelihood of collecting more species when more individuals were collected, species richness values were also compared after rarefaction (Simberloff, 1972) using EcoSim (Gotelli & Enstminger, 2001).

Multivariate ordination scores were used as a quantification of assemblage structure (Marsh-Matthews & Matthews, 2000). The structure of fish assemblages (*i.e.* constituent species and their relative abundances) was evaluated with correspondence analysis (CA), an indirect gradient analysis, using the programme CANOCO 4 (ter Braak & Šmilauer, 1998). Although there is evidence of the arch effect (Hill & Gauch, 1980) in the present analysis, detrending (DCA) was not performed due to the arbitrary and inconsistent nature of detrending algorithms (Jackson & Somers, 1991; Oksanen & Minchin, 1997). Species abundances were $\log_{10}(n+1)$ transformed to minimize the range and skew of distributions. Because diel occurrence patterns are more likely to be a sampling artefact for rare species than for common species, the rare species down-weighting option was employed (Hill & Gauch, 1980; ter Braak & Šmilauer, 1998).

RESULTS

A total of 41 604 individual fishes representing 134 species (Appendix) were collected. Characiforms made up 92% of the fish fauna sampled, and included 11 families, 45 genera and 94 species. Overall, the 23 most abundant species

accounted for 95% of the total catch, whereas 28 of the 134 fish species (21%) were only collected in a single sample. Sixty-two and 126 fish species were collected in diurnal and nocturnal samples, respectively. Eight species (6%) were collected only in diurnal samples, whereas 72 species (54%) were collected exclusively in nocturnal samples.

Of the 72 species collected only from nocturnal samples, 26 species (36%) were in >10% of nocturnal samples. Some of the species collected exclusively in nocturnal samples occurred abundantly (Fig. 2). For example, 3720 individual *Moenkhausia* sp. A were collected, with individuals present in every nocturnal sample (Appendix). Similarly, *Moenkhausia browni* Eigenmann, *Lonchogenys ilisha* Myers, *Acestrocephalus ginesi* Lasso & Taphorn, *Pimelodella* sp. A, *Moenkhausia lepidura* (Kner) and *Anchoviella* spp. were abundant in nocturnal collections, but were never present in diurnal samples. The eight fish species exclusively collected in diurnal samples occurred infrequently and in low abundances (Fig. 2 and Appendix). The most commonly collected, exclusively diurnal species, *Fluviphylax obscurus* Costa (Cyprinodontidae), was only present in three samples and represented by six individuals.

Species abundant in diurnal samples were small-bodied (<40 mm standard length, L_S), persistent residents of sandbanks. These fishes were predominantly diurnally active, fusiform, small-eyed characids [*e.g. Bryconamericus* sp., *Aphyocharax alburnus* (Günther) and *Rhinobrycon negrensis* Myers], a miniature catfish, *Imparfinis* sp., and the pygmy anchovy *Amazonsprattus scintilla* Roberts. Nocturnally abundant species included the common diurnal sandbank residents with the addition of small-bodied detritivores [*e.g. Caenotropus labyrinthicus* Kner, *Cyphocharax cf. leucostictus* (Eigenmann & Eigenmann) and *Cyphocharax cf. notatus* (Steindachner, 1908)], characids with deep bodies and large eyes (*e.g. Tetragonopterus chalceus* Spix & Agassiz), *L. ilisha* and *M. browni*), piscivorous characids (*e.g. A. ginesi, Acestrorhynchus minimus* Menézes and *Acestrorhynchus grandoculis* Menézes & Géry) and catfishes (*e.g. Pimelodella* sp. A, *Leptodoras* sp., *Pseudocetopsis* sp. and *Ochmacanthus alternus* Myers).



FIG. 2. Rank-abundance pattern of a neotropical freshwater assemblage with 136 species. –, species collected in both diurnal and nocturnal samples; ○, diurnal samples only; △, nocturnal samples only.

Distinct diel abundance patterns were also observed at the ordinal taxonomic level. Diurnal and nocturnal samples were both dominated by characiforms (Table I). Characiforms occurred in every diurnal and nocturnal sample, and comprised 80% and 97% of individual fishes, respectively, from these samples. Clupeiforms were twice as likely to be present in diurnal samples as nocturnal samples. Siluriforms were 55% more common in nocturnal samples than diurnal samples. Gymnotiforms occurred in 17% of nocturnal samples, but were never collected in diurnal samples. Perciforms were only slightly more common in nocturnal samples (73%) than diurnal samples (67%). The only cyprinodontiform, *F. obscurus*, and pleuronectiform, *Hypoclinemus mentalis* (Günther), were rare and only present in diurnal samples.

In addition to fishes, two species of shrimp, *Macrobrachium cf. dierythrum* (n = 1320) and *Acetes paraguayensis* (n = 2546), were collected in seine samples.

SPECIES RICHNESS

Species richness estimates did not differ among the seven sandbanks (ANOVA, d.f. = 5 and 6, P > 0.9); however, nocturnal samples were significantly more species rich (ANOVA, d.f. = 6 and 5, P < 0.014) than their paired diurnal samples [Fig. 1(a)]. After rarefaction, nocturnal samples still had significantly more species than diurnal samples (P < 0.05). The repeated measures interaction term between month and diel sampling period was not significant (ANOVA, d.f. = 36 and 30, P > 0.9), whereas the interaction between month and location was significant (ANOVA, d.f. = 30 and 36, P < 0.019), suggesting species richness values responded differently to rising and falling water levels among sandbanks. Overall, differences in species richness were weakly correlated with the annual flood pulse (Fig. 1). Sandbanks experienced an unexpected seasonal change due to colonization by filamentous algae and emergent macrophytes (e.g. Eleocharis sp. and Zanichellia cf. palustris) during high water months (June, October and November). Macrophyte growth was only observed on certain sandbanks, and samples from these locations had significantly more species (P < 0.019).

The number of individuals collected per sample varied considerably (range 13 to 1983), and differences between paired diel samples (ANOVA, d.f. = 6 and 5,

Order	Diurnal $(n = 48)$	Nocturnal $(n = 48)$
Clupeiformes (2)	46	23
Characiformes (94)	100	100
Gymnotiformes (3)	0	17
Siluriformes (19)	58	90
Cyprinodontiformes (1)	6	0
Perciformes (14)	67	73
Pleuronectiformes (1)	2	0

 TABLE I. Percentages of samples in which taxonomic orders occurred. Number of species per order is given in parentheses. Fish orders are organized phylogenetically according to Nelson (1994)

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P > 0.3) and among locations (ANOVA, d.f. = 5 and 6, P > 0.6) were not significant. Similarly, interactions between month and location (ANOVA, d.f. = 30 and 36, P > 0.7) or month and diel period within location (ANOVA, d.f. = 36 and 30, P > 0.2) were not significant when evaluating the number of individuals sampled.

ASSEMBLAGE STRUCTURE

Correspondence analysis revealed consistent differences in assemblage structure between diurnal and nocturnal samples (Fig. 3). The first four CA axes explained 40% of variation in assemblage structure [axis 1 eigenvalue = 0.307, (15% of variance explained); axis 2 eigenvalue = 0.248 (12%); axis 3 eigenvalue = 0.14 (7%); axis 4 eigenvalue = 0.107 (6%); total inertia = 2.025]. Sample scores on axis 1 were segregated by diel sampling period, and significantly correlated with the hour of day in which sampling occurred ($r^2 = 0.47$, P < 0.001). Axis 2 sample scores revealed a weaker correlation with hour of sampling ($r^2 = 0.14$, P < 0.001; Fig. 3). Assemblage structure was most variable among diurnal samples; diurnal samples ranged by 4.4 units on axis 1, whereas nocturnal samples ranged by 1.6 units on axis 1.

CASTNET SAMPLES

Twenty-four fish species represented by 499 individuals were collected in castnet samples. The four dominant species [*Hemiodus unimaculatus* (Bloch), *Brycon pesu* Müller & Troschel, *Biotodoma wavrini* (Gosse) and *Argonectes longiceps* (Kner)] made up 71% of the individuals collected. *Hemiodus unimaculatus*,



FIG. 3. Correspondence analysis ordination showing diel (○, diurnal and ●, nocturnal) periodicity in sandbank assemblage structure of the Cinaruco River, Venezuela. The first and second axes accounted for 15 and 12% of the variance in assemblage structure, respectively. Some symbols may represent more than one sample.

Boulengerella cuvieri (Spix & Agassiz), Brycon falcatus Müller & Troschel, silver dollar Myleus schomburgki (Jardine), Bryconops giacopinii (Fernández-Yépez), pike characin Acestrorhynchus microlepis (Schomburgk), M. lepidura, Curimatella immaculata (Fernández-Yépez) and Cichla orinocensis Humboldt were only collected in nocturnal seine samples, but all were collected on sandbanks in diurnal castnet samples. Four species collected with a castnet [Cichla temensis Humboldt, Myleus torquatus (Kenes), Paratrygon aiereba (Müller & Henle) and Hemiodus microlepis Kner] were never present in seine samples.

DISCUSSION

Assemblage composition and structure of nocturnal samples were consistently different from those of diurnal samples. Nocturnal samples were always more species rich than their corresponding diurnal samples [Fig. 1(a)], and nocturnal samples typically had more individual fishes than diurnal samples [Fig. 1(b)]. Sixty-eight per cent of the total fishes were collected in nocturnal samples. Based on rarefaction results, increases in nocturnal species richness were not simply a result of the larger number of individuals collected in nocturnal samples, but were caused by an influx of species onto the sandbanks after twilight.

A potential explanation of the differences between diel samples is that seine sampling was more efficient during nocturnal periods (Holland-Bartels & Dewey, 1997). Based on extensive sampling on sandbanks of this river using seines, castnets and other gears, differences in sampling efficiency seem unlikely to account for all of the observed differences in assemblage structure between nocturnal and diurnal samples. Comparisons between seine and diurnal castnet samples identify those taxa that probably avoided the seine during diurnal sampling. The relatively few species collected only during nocturnal sampling with the seine that also were collected diurnally with the castnet probably avoided capture by the seine diurnally. These species generally are large-bodied $(>100 \text{ mm } L_s)$ and fusiform, presumably fast swimmers. In contrast, most of the species collected exclusively in nocturnal samples were small-bodied (<100 mm) characids (e.g. Moenkhausia sp. A. M. browni, L. ilisha and A. ginesi) that seem unlikely to have avoided capture during daytime, and more likely reflect actual shifts in diurnal and nocturnal occupation of near-shore regions of sandbanks. Some of these small-bodied characids were among the most commonly collected species in nocturnal samples (Appendix). Diel patterns among rare species (<10 individuals, *i.e.* <0.02% total abundance, including eight species restricted to diurnal samples and 44 species restricted to nocturnal samples) are probably an artefact of random sampling error.

Many neotropical fishes are known to exhibit diel differences in habitat use (Lowe-McConnell, 1964). Fishes that occur on sandbanks during diurnal periods generally exploit sandbanks as a foraging habitat, and remain on sandbanks through the nocturnal period as a shallow-water refuge from predation. Previous research in marine and freshwater environments has documented a shoreward movement of predatory and prey fishes at nightfall (Helfman, 1981; Copp & Jurajda, 1993; Layman, 2000), with prey fishes generally occupying the

shallowest zones. In the Cinaruco River, diurnally active species, including those active on sandbanks as well as some from other macrohabitats, were nocturnally abundant in shallow sandbank waters. The species occupying sandbanks nocturnally may be exploiting sandbanks as a foraging habitat or a refuge from predation (Copp & Jurajda, 1993), and often exploit alternative habitat types during diurnal periods. Many of the fishes collected on sandbanks exclusively in nocturnal samples also were collected in diurnal samples of submerged woody debris and leaf litter in a concurrent study on the same river (unpubl. data). For example, in the present study the tetras Moenkhausia copei (Steindachner) and Hemigrammus vorderwinkleri Géry were collected frequently but exclusively in nocturnal samples (69 and 46% of nocturnal samples, respectively). Based on additional sampling in alternative habitats, these species were characterized diurnally as being associated with structurally complex habitats (e.g. leaf litter). In addition, nocturnally active species [e.g. Leptodoras sp. and the glass knifefish Eigenmannia virescens (Valenciennes)] that often occupy deep channel areas diurnally (Stewart et al., 2002) were found to exploit shallow water sandbank habitats nocturnally. Unfortunately, in the present study it was not possible to unequivocally identify if species were using habitats as a refuge from predation or a site for feeding.

Diel patterns in assemblage composition seem to be associated with morphological trade-offs in foraging and anti-predator defenses. Many nocturnal species possess morphological specializations for activity in light-limited settings. Weakly electric fishes (Gymnotiformes) can perceive their surroundings and locate prey using electrosensory cues (Lundberg et al., 1987). This sensory capability facilitates nocturnal activity and occupation of turbid waters with low light levels (Rodríguez & Lewis, 1997; MacIver et al., 2001). Similarly, catfishes, most of which rely heavily on tactile and chemical cues when foraging (Pohlmann et al., 2001), were common members of the nocturnal assemblage. Gymnotiforms and siluriforms, previously characterized as members of the deep-river assemblage (Lundberg et al., 1987; Stewart et al., 2002), were collected in shallow, shoreline areas nocturnally. Among characiforms collected exclusively in nocturnal samples, several species have large eves that presumably enhance visual acuity in light-limited settings (Shand, 1997). At present, it is unclear if this attribute is an adaptation primarily for foraging in deep waters where light is limited diurnally (Stewart et al., 2002), or for foraging in shallow waters where light is limited nocturnally, or both.

Responses of species to physical habitat features (*e.g.* light levels, habitat complexity and water depth) and biotic interactions (*e.g.* competition and predation) are expected to yield patterns of activity and habitat use that maximize fitness (Burrows *et al.*, 1994; Gibson *et al.*, 1998). In marine systems, diel differences in activity and habitat use may be produced by diel periodicity in foraging activity, predator avoidance and interaction between the two (Robblee & Zieman, 1984; Burrows *et al.*, 1994; Gibson *et al.*, 1998). Diel patterns of habitat occupancy and foraging activity observed in the present study are consistent with predator-avoidance behaviour. Diurnally active piscivores on sandbanks include fishes (*e.g. Cichla* spp., *Boulengerella* spp. and *Serrasalmus* spp.) and birds (*e.g.* kingfishers, skimmers, terns; D.A. Arrenglon, pers. obs.). Nocturnal piscivores include catfishes (*e.g. Pseudoplatystoma fasciatum* L.), and

some characins (*e.g. A. ginesi* and *A. grandoculis*). Lowe-McConnell (1964) speculated that diurnally active fishes avoid piscivorous catfishes at night by remaining motionless within structurally complex habitats in shallow water. Recently it has been shown that catfishes can locate prey in the absence of visible light by detecting and tracking turbulence along swim paths (Pohlmann *et al.*, 2001). The composition of piscivore assemblages in Orinoco floodplain lakes depends, in part, on water transparency and light penetration (Rodríguez & Lewis, 1997). In the Cinaruco River, diel changes in ambient light intensity are clearly associated with foraging periodicity of dominant piscivores (*e.g. Cichla* and *Serrasalmus* spp. feeding by day and large pimelodid catfishes by night), which may influence temporal dynamics of prey fish assemblage structure on sandbanks.

In the Cinaruco River, diurnal and nocturnal samples taken at the same locations, on average 5 days apart, had divergent species composition and relative abundances. Nocturnal samples were more similar to nocturnal samples on different sandbanks than they were to diurnal samples collected on the same sandbank. In spite of the large magnitude of seasonal variation in hydrology and habitat availability in the Cinaruco River, species richness and abundance varied relatively little within the two diel periods (Fig. 1). Fish densities were expected to be highest at the beginning of the dry season (January), and to decline throughout the dry season in response to increased predation rates in reduced volumes of aquatic habitat (Winemiller, 1989; Jepsen et al., 1997; Winemiller & Jepsen, 1998). Diurnal and nocturnal species richness and nocturnal abundance followed this expected trend; however, diurnal abundance did not show this pattern. The largest seasonal change in species richness observed on sandbanks was an increase in the number of species collected from sandbanks that had become colonized by filamentous algae and emergent macrophytes during high water months (June, October and November). In temperate systems, aquatic vegetation provides refuge from predation and food resources for algivorous and invertivorous fishes (Werner et al., 1983; Burke et al., 2001). Alternatively, algae and macrophytes could have increased sampling efficiency of the seine, but this explanation seems less likely than the former.

Documentation of biological diversity, particularly in tropical habitats, is a major goal of conservation biology (Lawton *et al.*, 1998; Ehrlich, 2002). Such efforts frequently produce baseline taxonomic inventories used to prioritize areas for conservation (Toledo-Piza *et al.*, 2001). Findings from the present study highlight the importance of nocturnal sampling in these efforts. Nocturnal samples contained 94% of all of the species collected from shallow sandbank habitats of the Cinaruco River, and 54% of these species were exclusively collected in nocturnal samples. Biological inventories of neotropical fresh waters should include both diurnal and nocturnal collections.

The National Geographic Society (KOW), the L.T. Jordan Institute (DAA), and the International Sportfish Fund (KOW and DAA) provided funding for this research. DAA was supported as a Tom Slick Senior Graduate Fellow during the writing of this manuscript. The Servicio Autonomo de Los Recursos Pesqueros y Acuicolas (SARPA) of Venezuela provided scientific fishing permit #0192. D. Taphorn provided taxonomic and logistic assistance throughout this study, and the Museo de Ciencias Naturales staff in Guanare was very helpful. The Stergios family extended generous hospitality during stays

in Guanare. G. Webb and C. Lofgren of Tour Apure and E. Pelaez and J. Marzuola of the Cinaruco River Fishing Club provided housing and logistical assistance while in the field. C. Garcia, J. Garcia, B. Payton and C. Layman assisted in field collections. J. Arrington provided invaluable assistance with field collections and enumeration of specimens. J.V. Montoya identified the shrimps.

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APPENDIX. Species cc Values show	llected in near-shore sa n are the number of inc	ndbank seine samples. Species are soi lividuals collected (abundance) and p	rted by rank (tak er cent of sample	ten from rank-a es in which the	bundance gr species occur	aph, Fig. 2). red
Order	Family	Species	Abundance	All samples	Diurnal	Nocturnal
Characiformes	Characidae	Bryconamericus sp. A	5215	0.97	52.1	100.0
Characiformes	Characidae	Hemigrammus schmardae	4978	54.2	8.3	100.0
Characiformes	Hemiodontidae	Bivibranchia fowleri	4493	89-6	81.3	6.79
Characiformes	Characidae	Moenkhausia sp. A	3720	50.0	$0 \cdot 0$	100.0
Characiformes	Characidae	Aphyocharax alburnus	3124	93.8	89.6	6.79
Characiformes	Characidae	Rhinobrycon negrensis	2905	78.1	64.6	91.7
Clupeiformes	Engraulidae	Amazonsprattus scintilla	2498	30.2	45.8	14.6
Characiformes	Characidae	Microschemobrycon callops	2133	54·2	14.6	93·8
Characiformes	Characidae	Microschemobrycon casiquiare	1769	46.9	25.0	68·8
Characiformes	Characidae	Hemigrammus analis	1550	43.8	20.8	66.7
Characiformes	Characidae	Bryconops caudomaculatus	1257	74.0	47-9	100.0
Characiformes	Characidae	Creagrutus phasma	1171	59-4	37-5	81·3
Characiformes	Characidae	Hemigrammus vorderwinkleri	805	33·3	20.8	45.8
Characiformes	Characidae	Knodus cf. heteresthes	699	44·8	14.6	75.0
Characiformes	Characidae	Hemigrammus sp. A	607	10.4	10.4	10.4
Characiformes	Characidae	Moenkhausia browni	573	37.5	0.0	75.0
Characiformes	Characidae	Moenkhausia copei	491	40.6	12.5	68·8
Characiformes	Characidae	Hemigrammus micropterus	428	18.8	6.3	31.3
Characiformes	Characidae	Moenkhausia cf. ceros	401	29·2	8·3	50.0
Siluriformes	Pimelodidae	Imparfinis sp.	238	56.3	43.8	68·8
Characiformes	Crenuchidae	Characidium sp. A	226	28.1	35-4	20.8
Perciformes	Cichlidae	Geophagus sp.	181	52.1	47-9	56.3
Characiformes	Characidae	Hemigrammus elegans	164	17.7	$2 \cdot 1$	33-3
Characiformes	Characidae	Lonchogenys ilisha	112	19.8	0.0	39.6
Characiformes	Curimatidae	Cyphocharax spilurus	105	4·2	$2 \cdot 1$	6.3
Characiformes	Characidae	Hemigrammus sp. B	105	4·2	6.3	$2 \cdot 1$

Order	Family	Species	Abundance	All samples	Diurnal	Nocturnal
Characiformes	Characidae	Acestrocephalus ginesi	103	20.8	0.0	41.7
Siluriformes	Doradidae	Trachydoras cf. microstomus	102	10.4	$2 \cdot 1$	18.8
Characiformes	Characidae	Bryconamericus sp. B	91	$28 \cdot 1$	$2 \cdot 1$	54·2
Perciformes	Cichlidae	Biotodoma wavrini	80	18.8	10.4	27.1
Siluriformes	Pimelodidae	Pimelodella sp. A	64	16.7	$0 \cdot 0$	33-3
Characiformes	Characidae	Serrasalmus spp.	63	4·2	4·2	4·2
Perciformes	Cichlidae	Satanoperca daemon	09	7.3	6.3	8.3
Characiformes	Characidae	Hyphessobrycon bentosi	59	8·3	$2 \cdot 1$	14.6
Characiformes	Characidae	Moenkhausia lepidura	55	14.6	$0 \cdot 0$	29.2
Characiformes	Characidae	Acestrorhynchus minimus	49	15.6	0.0	31.3
Characiformes	Characidae	Parapristella georgiae	46	9.4	$2 \cdot 1$	16.7
Clupeiformes	Engraulidae	Anchoviella sp.	43	6.3	$0 \cdot 0$	12.5
Siluriformes	Pimelodidae	Pimelodella sp. B	42	12.5	$2 \cdot 1$	22.9
Perciformes	Cichlidae	Apistogramma sp. A	40	15.6	14.6	16.7
Characiformes	Curimatidae	Cyphocharax oenas	40	5.2	4·2	6.3
Characiformes	Curimatidae	Cyphocharax cf. leucostictus	39	8·3	$0 \cdot 0$	16.7
Characiformes	Characidae	Acestrorhynchus grandoculis	36	14.6	$0 \cdot 0$	29.2
Characiformes	Characidae	Bryconops alburnoides	32	12.5	4·2	20.8
Characiformes	Chilodontidae	Caenotropus labyrinthicus	29	12.5	0.0	25.0
Characiformes	Characidae	Hemigrammus sp. C	27	5.2	0.0	10.4
Characiformes	Characidae	Hemigrammus stictus	27	3.1	$2 \cdot 1$	4.2
Characiformes	Characidae	Tetragonopterus chalceus	26	11.5	0.0	22.9
Characiformes	Crenuchidae	Characidium sp. B	23	8·3	12.5	4·2
Characiformes	Characidae	Brycon falcatus	22	12.5	0.0	25.0
Characiformes	Characidae	Brycon pesu	22	16.7	6.3	27.1
Characiformes	Curimatidae	Curimatopsis evelynae	20	4·2	$2 \cdot 1$	6.3
Siluriformes	Doradidae	Leptodoras sp. A	20	3.1	0.0	6.3

APPENDIX. Continued overleaf

Order	Family	Species	Abundance	All samples	Diurnal	Nocturnal
Characiformes	Characidae	<i>Moenkhausia</i> sp. B	5	$1 \cdot 0$	$0 \cdot 0$	2.1
Characiformes	Characidae	Oxybrycon parvulus	5	3.1	0.0	6.3
Characiformes	Hemiodontidae	Argonectes longiceps	4	$2 \cdot 1$	4.2	0-0
Characiformes	Characidae	Hemigrammus bellottii	4	$1 \cdot 0$	$2 \cdot 1$	0.0
Perciformes	Cichlidae	Heros sp.	4	$2 \cdot 1$	$2 \cdot 1$	$2 \cdot 1$
Siluriformes	Doradidae	Leptodoras sp. B	4	$1 \cdot 0$	0.0	2.1
Perciformes	Cichlidae	Mesonauta insignis	4	3.1	$2 \cdot 1$	4.2
Characiformes	Characidae	<i>Moenkhausia</i> sp. C	4	$2 \cdot 1$	0.0	4·2
Characiformes	Lebiasinidae	Nannostomus unifasciatus	4	4.2	0.0	8.3
Characiformes	Prochilodontidae	Semaprochilodus kneri	4	4.2	0.0	8.3
Perciformes	Cichlidae	Cichla spp.	ω	3.1	4.2	$2 \cdot 1$
Characiformes	Curimatidae	Curimatopsis sp.	б	3.1	4.2	$2 \cdot 1$
Characiformes	Characidae	Hemigrammus cf. tridens	б	$2 \cdot 1$	0.0	4.2
Characiformes	Characidae	Hemigrammus rhodostomus	ŝ	$2 \cdot 1$	$2 \cdot 1$	2.1
Characiformes	Hemiodontidae	Hemiodus unimaculatus	ω	$2 \cdot 1$	0.0	4.2
Perciformes	Cichlidae	Hoplarchus psittacus	б	$2 \cdot 1$	$2 \cdot 1$	2.1
Characiformes	Characidae	Myleus spp.	б	3.1	$2 \cdot 1$	4·2
Siluriformes	Trichomycteridae	Ochmacanthus orinoco	б	$2 \cdot 1$	0.0	4.2
Siluriformes	Pimelodidae	Pimelodus blochi	ŝ	3.1	0.0	6.3
Perciformes	Cichlidae	Acaronia vultuosa	2	$2 \cdot 1$	0.0	4.2
Perciformes	Cichlidae	Biotoecus dicentrarchus	2	$2 \cdot 1$	4.2	0.0
Characiformes	Crenuchidae	Characidium sp. C	2	1.0	$2 \cdot 1$	0.0
Gymnotiformes	Rhamphichthyidae	Gymnorhamphichthys hypostomus	7	$2 \cdot 1$	0.0	4.2
Characiformes	Characidae	Hemigrammus microstomus	2	$1 \cdot 0$	0.0	$2 \cdot 1$

APPENDIX. Continued overleaf

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Heterocharax macrolepis Myleus rubripinnis Myleus schombureki	Potamorhina sp. Pyrrhulina lugubris Trichomycterus sp.	Acestrorhynchus sp. Acestrorhynchus falcirostris Anostonuus ternetzi Anistooramma sp. B.	Asiphonichthys condei Cichla orinocensis	Copella metae Hemiodus immaculatus	Hemiodus semitaeniatus Hvpoclinemus mentalis	Hypopygus lepturus Iguanodectes spilurus	Leporinus brunneus Metynnis hypsauchen	Microglanis poecilus Moenkhausia sp. D	Psectrogaster ciliata Rineloricaria sp.	Serrasalmus rhombeus	Centromochlus concolor Thayeria obliqua
Characidae Characidae Characidae	Curimatidae Lebiasinidae Trichomvoteridae	Characidae Anostomidae Cichlidae	Characidae Cichlidae	Lebiasinidae Hemiodontidae	Hemiodontidae Achiridae	Hypopomidae Characidae	Anostomidae Characidae	Pimelodidae Characidae	Curimatidae Loricariidae	Characidae	Auchenipteridae Characidae
Characiformes Characiformes Characiformes	Characiformes Characiformes Siluriformes	Characiformes Characiformes Perciformes	Characiformes Perciformes	Characiformes Characiformes	Characiformes Pleuronectiformes	Gymnotiformes Characiformes	Characiformes Characiformes	Siluriformes Characiformes	Characiformes Siluriformes	Characiformes	Siluritormes Characiformes