Seasonal and diel variation of shrimp (Crustacea, Decapoda) on sandbanks of a tropical floodplain river

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Published online: 22 Jan 2014.

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We studied seasonal and diel changes of shrimp abundance in sandbanks of the Cinaruco River, a tropical floodplain tributary of the Orinoco River. Paired diurnal and nocturnal samples were collected from seven river-channel sandbanks during different periods of an annual hydrological cycle. We collected 3730 shrimp representing two families: Sergestidae (*Acetes paraguayensis*) and Palaemonidae (six species). Patterns of temporal and spatial variation of shrimp abundance on sandbanks of the Cinaruco indicated responsiveness to both diurnal cycles and the annual hydrological regime. The presence of submerged vegetation and the absence of ridge-and-trough topography on sandbanks were the factors most strongly associated with high shrimp abundance. We conclude that the river's seasonal flow regime and geomorphology create the heterogeneity of hydraulic habitats that is essential for diel movements of shrimp between areas used for nocturnal foraging and diurnal refuge.

Keywords: *Acetes paraguayensis*; benthos; habitat; Palaemonidae; Orinoco

Introduction

Freshwater shrimp are a major component of community biomass in tropical and subtropical rivers (Odinetz-Collard 1987; Nessimian et al. 1998; Richardson and Cook 2006) and also play major roles within river food webs (Covich et al. 1999; Dudgeon 1999; Collins et al. 2007a). In tropical forested streams, shrimp contribute to spatial heterogeneity of benthic resources (Pringle et al. 1993; Pringle 1996), and have been shown to link food webs of different habitats via active migration or passive drift (March et al. 1998; Montoya 2003; Bauer 2011). In rivers with seasonal flow regimes, movement by shrimp among aquatic habitats may be important for population persistence (Walker 1992; Moreira and Odinetz-Collard 1993; Odinetz-Collard and Magalhães 1994; Lytle and Poff 2004).

To date, most research on freshwater shrimp ecology in the tropics has been conducted in forest streams, and to the best of our knowledge, there are no published studies on the ecology of shrimp in sandbank habitats of large tropical rivers, the focus of the present study. Lowland rivers and floodplains in the tropics support high biodiversity and productivity in a dynamic, heterogeneous landscape (Junk et al. 1989; Winemiller 1996; Amoros and Bornette 2002; Montoya et al. 2011).

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Hydrological and hydraulic variability maintains physical habitat diversity in the floodplain landscape ("shifting habitat mosaic" of Stanford et al. 2005). Hydrological connectivity, which is influenced by fluvial geomorphology and flow regime, maintains biodiversity and ecosystem services, including sediment and nutrient dynamics as well as primary and secondary production (Ward and Stanford 1995; Poff et al. 1997; Amoros and Bornette 2002; Pringle 2003; Charlton 2008).

One of the most prominent features of meandering floodplain rivers is the presence of sandbanks that are formed on channel bends (point bars). Sandbanks act as natural bioreactors that transform different forms of nitrogen as water moves through the interstices (Fisher et al. 2001). Although sandbanks are relatively consistent features at large scales, individual sandbanks have environmental variation at smaller scales that influences the ecology of small fish and invertebrates. The mobility of sand, resulting in the continual formation of bed forms such as ripples and sand waves, yields structural complexity at a fine spatial scale (Kellerhals and Church 1989; Howard 1992; Gordon et al. 2004; Strayer et al. 2006; Charlton 2008).

The present study investigates seasonal and diel patterns of abundance of freshwater shrimp on sandbanks of the Cinaruco River, a meandering floodplain river within the Orinoco River Basin in Venezuela. We also document relationships between abundance patterns for two coexisting shrimp families (Palaemonidae and Sergestidae) and environmental variables in a habitat that has relatively low structural complexity and heterogeneity within the main channel of large rivers. We hypothesized that seasonal patterns in shrimp abundance on sandbanks would be associated with seasonal changes in habitat that influence the availability of food resources and suitability of the habitat as a refuge from predation. We anticipated that lowest shrimp abundances would correspond to low-water months of the annual hydrological cycle when resource availability decreases and predator densities increase. During periods when water levels are higher, shrimp should be more abundant on sandbanks because there are greater inputs of allochthonous food resources, structural complexity of the littoral increases due to the presence of submerged macrophytes, and predator densities decline on sandbanks as many fish become dispersed into flooded riparian areas.

Material and methods

Study site

This study was performed in the Cinaruco River, a clear-water, lowland tributary of the Orinoco River located in Apure State, southwestern Venezuela. Cinaruco is an oligotrophic river (very low nutrient concentration), relatively transparent (1.1–2.1 m Secchi disk depth), with very low conductivity (~ 6 μS/cm), and moderately acidic waters (pH 5–7). A detailed description of the landscape and limnological features of the Cinaruco River appears in Montoya et al. (2006) and Roelke et al. (2006). Surveys were performed in an 8-km reach of the main channel located approximately 55 km upstream of the river's confluence with the Orinoco. This reach has high geomorphological heterogeneity, including pronounced river sinuosity and broad sandbanks (point bars) on the inside of each major bend of the river, and lateral sandbanks located along the margins in other stretches with relatively slow water

velocities. Sandbanks vary in spatial extent and slope, with sands shifting in response to hydraulic conditions that change with seasonal discharge; high-flow periods are dynamic and low-flow periods tend to be stable. Point sandbanks on bends of the Cinaruco tend to be larger than lateral sandbanks. Landscape heterogeneity in this reach also is increased by main channel backwaters, side channels, floodplain lagoons and creeks. Among floodplain lagoons along the studied 8-km reach of the river, Laguna Larga is the largest and is continuously open to the main channel of Cinaruco year-round. Water-level readings were taken on a limnimeter located in Laguna Larga on a daily basis.

Sampling

Shrimp samples for analysis were collected during 1999. The study design consisted of paired diurnal and nocturnal samples that were collected on a monthly basis from February to June (low-water and rising-water seasons) and from November to December (falling-water season). No samples were collected between July and October (high-water season) because the sandbanks were inundated. Samples were collected by seining seven main-channel sandbanks using a 6.4 m × 1.8 m seine (4-mm mesh). Sandbanks were located along a river segment centred at approximately 6°33′ N, 67°24′ W. Sandbanks 1, 2, 4 and 5 were point bars, whereas sandbanks 3, 6 and 7 were lateral banks (Figure 1).
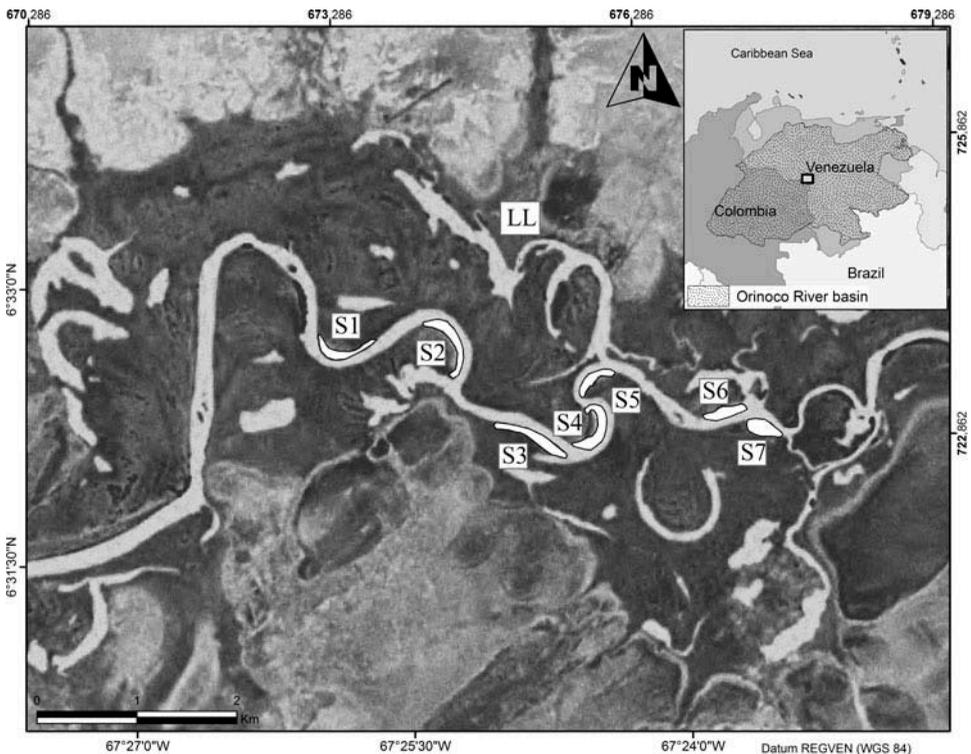

Figure 1. Locations of sampling sites on Cinaruco River near Laguna Larga (LL). Sampled sandbanks are shown with codes from S1 to S7. This NASA LandSat image was taken during the dry season of 2000.

At each sandbank, three contiguous, non-overlapping 10-m hauls were made parallel to the shore, and then combined to comprise a sample. During each month, diurnal samples (between 09.00 and 16.00 h) were taken from seven sandbars over a 2-day period. Nocturnal sampling (between 21.30 and 02.00 h) was performed on a single night within 3–6 days of the corresponding diurnal sampling in the same area. No samples were taken at sandbar 3 during November 1999.

Environmental variables, including depth, current velocity (measured with a mechanical flowmeter), temperature and dissolved oxygen (both measured with a YSI 85 meter) were recorded at sites on each survey date. Percentage substrate coverage of leaf litter was estimated visually. Presence/absence of ridge-and-trough topography, fine particulate organic matter (FPOM), and submerged vegetation were recorded qualitatively by assigning a value of zero for absence and a value of one or two for sparse/moderate or abundant presence, respectively, in the sampled area. Submerged vegetation consisted of irregular patches of the aquatic plant *Zannichellia* sp. (Alismatales: Potamogetonaceae). A ridge-and-trough topography comprised the presence of a series of ridges running parallel or diagonal to the shore and interspersed with shallow troughs or troughs. Additionally, the illuminated fraction of the moon (from 0 to 1) during nocturnal surveys was obtained from the Astronomical Applications Department of the US Naval Observatory (USNO) website at http://aa.usno.navy.mil/data/docs/MoonFraction.php

Shrimp specimens were identified in the field to family level (Palaemonidae or Sergestidae) and counted. Specimens were killed by submersion in a solution of tricaine methanesulphonate (125 mg/l) before fixation in 10% formalin and subsequent preservation in 70% ethanol. In the laboratory, adult specimens were used to identify species according to taxonomic authorities (Kensley and Walker 1982; Pereira 1986; López and Pereira 1996; D'Incao and Martins 2000; García-Dávila and Magalhães 2003).

Data analyses

Shrimp abundance was expressed as the number of individuals per sample. A sample comprised three contiguous, non-overlapping 10-m hauls using a 6.4 m × 1.8 m seine. Diel variation in abundance of palaemonid shrimp was compared using the Wilcoxon signed-rank test; no sergestids were collected on sandbanks during daylight surveys. Due to the low number of palaemonids collected during daylight, only nocturnal samples were subsequently analysed for relationships among shrimp family abundance and environmental variables.

Spatio-temporal variation of shrimp family abundances (i.e. among sandbanks and months) was assessed using a permutation-based, non-parametric multivariate analysis of variance (PERMANOVA; Anderson 2001; McArdle and Anderson 2001; McCune and Grace 2002). Effects of location (sandbank) and date (month) were tested with an experimental design based on an unreplicated, two-factor crossed PERMANOVA in which experimental units (sandbanks) are sampled repeatedly through time (months). Under this design (similar to a randomized, complete-block design), in which there is only one replicate in every treatment–block combination (any sandbank–month combination), there is no formal test for the interaction term (sandbank × month). In fact, this model assumes that there is no interaction between factors. However, there are several ways to test for interaction in this type of

experimental design. One of these is graphical, using interaction plots (Quinn and Keough 2002). For each of the two response variables in the present design (palaemonid and sergestid abundances), we graphically determined that there was no interaction (sandbank × month) using interaction plots (plots not shown). PERMANOVA was run using the software PC-ORD (version 5.10, MJM software, Gleneden Beach, OR, USA) (McCune and Mefford 2006).

The ENVFIT function in the VEGAN package in R 2.15.0 (Oksanen et al. 2012) was used to relate continuous (vectors) and categorical (factors) environmental variables to the matrix of shrimp abundances. The matrix consisted of standardized abundances of *Acetes paraguayensis* and palaemonids for all sites and sampling dates (excluding cases with no shrimp). Standardization of abundance data was based on the logarithmic transformation suggested by Anderson et al. (2006). Six continuous variables: depth (m), current velocity (m/s), temperature (°C), dissolved oxygen (mg/l), leaf litter cover (%) and illuminated moon (%); and two categorical variables: vegetation (absent, moderate and abundant), and FPOM (visibly absent versus present) were included in the analysis. Ridge-and-trough topography, as a measured categorical variable, was omitted from the analysis because of its high correlation with vegetation (Spearman's $r = -0.66$). The maximum correlation between continuous variables and the shrimp abundance matrix was achieved through vector fitting in ENVFIT. The probability of obtaining an equal or larger correlation from random data (p) was estimated from 999 permutations. For categorical variables, the ENVFIT function fits a centroid to each level of a variable and then calculates a correlation coefficient as a measure of separation among the different levels of that variable. Values of p were also obtained from 999 random permutations. Finally, abundance data for sergestid and palaemonid shrimp were pooled across all survey locations and dates to view the relationships of abundance with three levels of vegetation and ridge-and-trough topography (absent, low or abundant).

Results

Taxonomic diversity and abundance

Surveys produced 3730 shrimp representing seven species, four genera and two families (Table 1). One species appears to be an undescribed species of *Pseudopalaemon*, and is hereafter designated as *Pseudopalaemon* "sp1". Palaemonid shrimp were more abundant in night samples than day samples (Wilcoxon signed-rank test, $Z = -3.51$, $n = 48$, $p < 0.001$, Figure 2). Among adult palaemonids, *Macrobrachium dierythrum*, *Palaemonetes carteri* and *Pseudopalaemon gouldingi* were always more abundant than *Pseudopalaemon chryseus*, *Pseudopalaemon amazonensis* and *Pseudopalaemon* sp1. Although it was possible to identify most adult palaemonids, several specimens could not be identified due to the lack of diagnostic characters (juvenile or incomplete specimens). The planktonic sergestid *Acetes paraguayensis* was only present in nocturnal samples. Subsequent surveys conducted in 2001–2003, 2009–2010 and 2013 on sandbanks of the Cinaruco did not yield additional shrimp taxa.

PERMANOVA showed that shrimp abundance on sandbanks was significantly associated with location (sandbars) and season (months) (Table 2). Abundance of the

Table 1. Checklist of freshwater shrimp (Crustacea: Decapoda)* collected from sandbanks of the Cinaruco River.

Suborder DENDROBRANCHIATA
Family SERGESTIDAE
Acetes paraguayensis Hansen, 1919
Suborder PLEOCYEMATA
Infraorder CARIDEA
Family PALAEMONIDAE
Macrobrachium dierythrum Pereira, 1986
Palaemonetes carteri Gordon, 1935
Pseudopalaemon amazonensis Ramos Porto, 1979
Pseudopalaemon chryseus Kensley and Walker, 1982
Pseudopalaemon gouldingi Kensley and Walker, 1982
Pseudopalaemon sp1.[†]

Notes: *Classification based on De Grave et al. (2009).
[†]Undescribed species.

sergestid peaked during May–June, and abundance of palaemonids peaked during November–December. During low-water months (February to April), shrimp were less abundant (Figure 2). May and June are the months when the water level rises in the Cinaruco (the beginning of the annual flood pulse). During this period, littoral areas, including main channel sandbanks, are rapidly inundated and heterogeneity of littoral areas increases. During November and December, when the water level falls, the landscape changes more gradually than it does during May and June. During the falling-water period, the tops of sandbanks start to emerge after 4 months of submergence.

When all sampling dates were pooled together, shrimp abundance varied significantly among sandbanks (Figure 3). The sergestid was most abundant on sandbanks 2, 4 and 5, whereas palaemonids were more abundant on sandbanks 1 and 5. Sandbanks 3, 6 and 7 had low shrimp abundance.

Shrimp–habitat relationships

Environmental variables varied seasonally. Submerged vegetation was absent during February and March, and during April was only present on sandbank 2. Presence of vegetation was important in June and November, especially on point sandbanks. Submerged vegetation patches were almost absent from lateral sandbanks. This seasonal appearance of submerged vegetation is a recurrent annual event on main channel point sandbanks (vegetation has not been observed on any other habitat on the main channel or lagoons). Macrophyte patches disappear entirely during the low-water periods. Percentage of leaf litter coverage varied between 0 and 20% for all months and sandbanks, with the exception of November when values averaged 24% (ranging from 0 to 65%) for sampled sandbanks. FPOM was visibly absent during February, November and
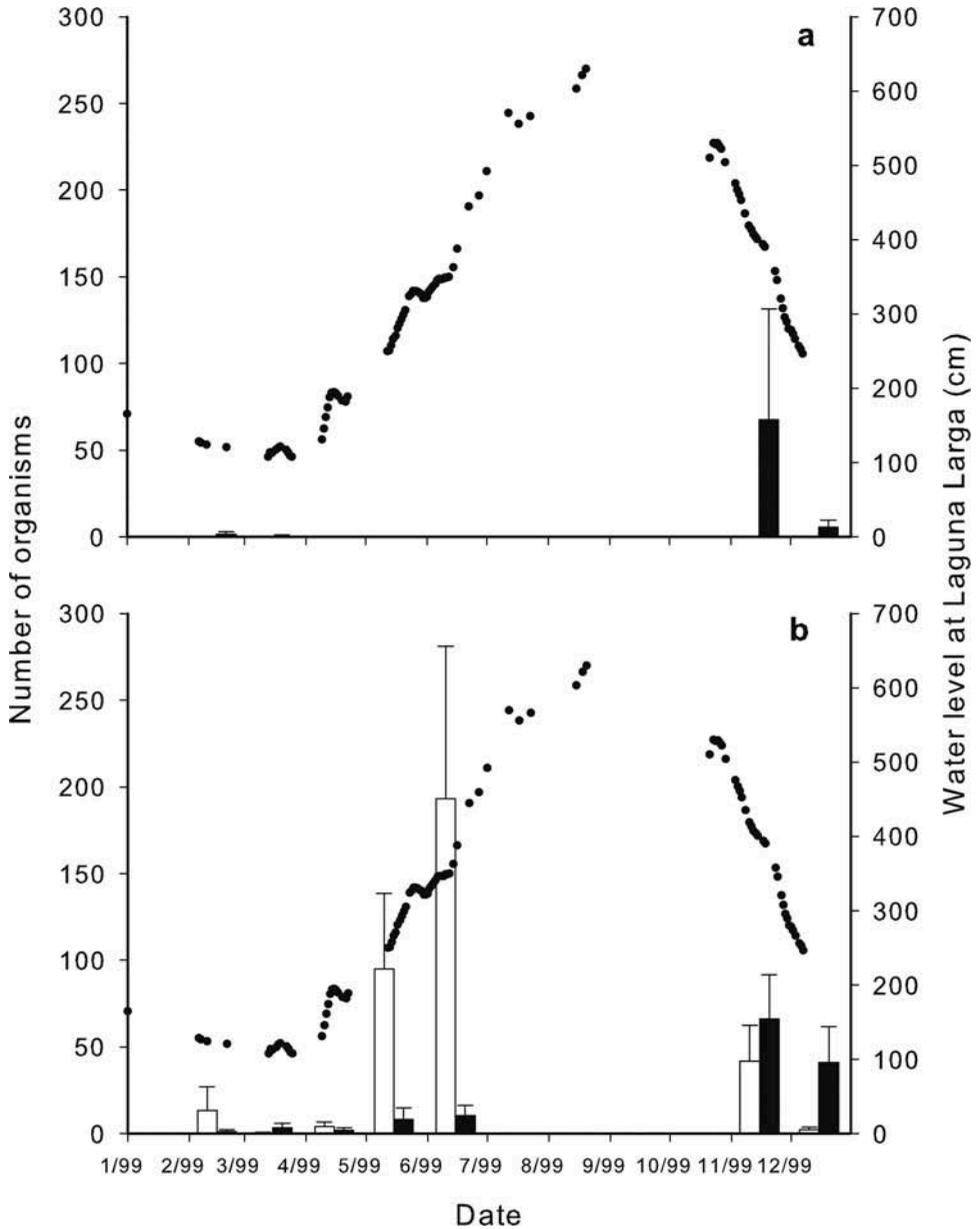
Figure 2. Seasonal variation of mean number of sergestid (empty bars) and palaemonid (filled bars) shrimp in diurnal (A) and nocturnal (B) samples from sandbanks of the Cinaruco River during 1999 (mean + SE). $n = 7$, except in November when only six sandbanks were sampled. No samples were taken during January or from July to October. A smoothed hydrograph of the Cinaruco River is superimposed to show water level variation during 1999.

December; but its presence on sandbanks during the rest of the sampling months was highly variable. The fraction of illuminated moon was below 0.04 except in March (0.273), May (0.157) and November (0.393).

Table 2. Two-factor crossed permutation-based, non-parametric multivariate analysis of variance (PERMANOVA) evaluating differences in shrimp (*Acetes paraguayensis* plus palaemonids) abundance between sandbanks and months. This design is similar to a randomized complete block configuration in which each combination of factors is unreplicated.

Source	d.f.	SS	MS	F	*p**
Sandbank	6	158100	26349	3.044	0.0002
Month	6	237420	39570	4.56	0.0002
Residual	36	312230	8673.1		
Total	48	707750			

Notes: *Randomization test of significance of pseudo *F* values based on 4999 randomizations.
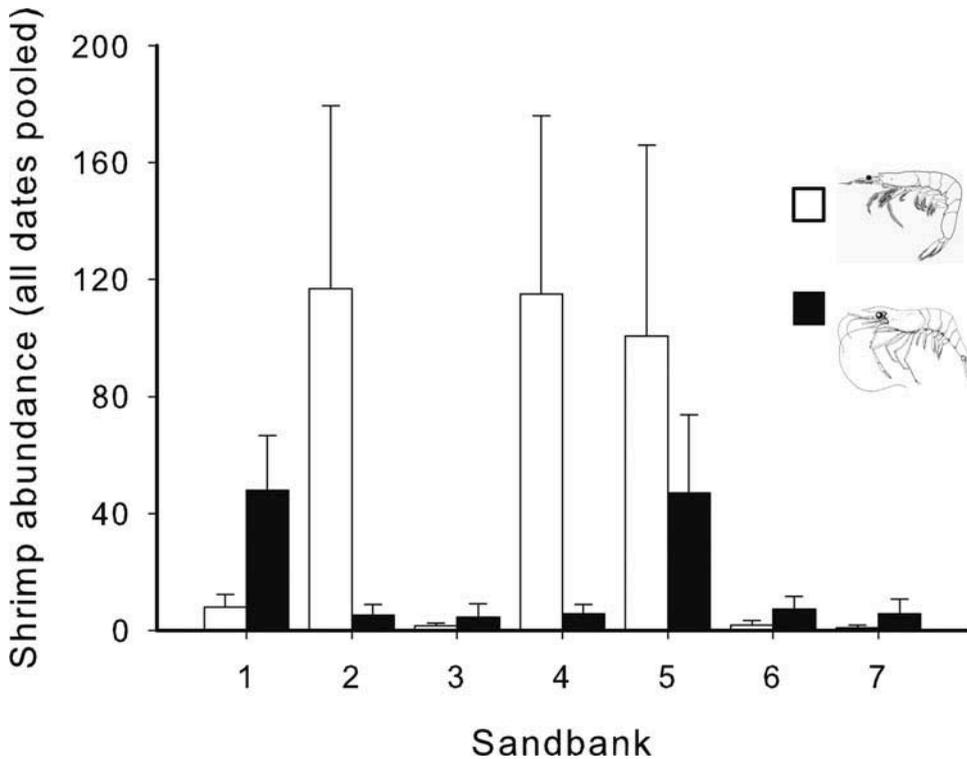
Figure 3. Abundance (mean + SE) of *Acetes paraguayensis* (empty bars) and palaemonids (filled bars) from sandbanks of the Cinaruco River during 1999 (pooling all sampling dates together) *n* = 7, except sandbank 3 (sampled only six times).

Water temperature ranged between 28.2°C and 32.9°C, with lowest values recorded during June and the highest in December. Dissolved oxygen had highest values (7.4 ± 0.4 mg/l, range: 6.75–8.09 mg/l) during low-water months and was lowest during November–December (5.94 ± 0.45 mg/l, range: 5.38–6.67 mg/l). Current velocity on sandbanks varied between 0 and 0.43 cm/s across all months.

Table 3. Environmental vectors (continuous variables) and factors (categorical variables) significantly correlated with shrimp abundance based on the *envfit* procedure.

Variable	r	p*
Vectors		
Depth	0.20	0.493
Current velocity	0.37	0.107
Temperature	0.49	0.008**
Dissolved oxygen	0.44	0.040*
Leaf litter	0.41	0.036*
Moon illumination	0.14	0.702
Factors		
Vegetation	0.52	0.001***
Fine particulate organic matter	0.235	0.144

Note: *p-values based on 999 random permutations.

Submerged vegetation (plus temperature, dissolved oxygen and, to a lesser extent, leaf litter) was associated with spatiotemporal patterns of shrimp abundance (Table 3). Shrimp abundance was strongly and positively associated with the presence of vegetation, and also with the absence of ridge-and-trough topography, given the strong inverse relationship between these two variables.

A significant seasonal trend was observed for submerged vegetation and ridge-and-trough topography. Most sandbanks that were point bars (1, 2, 4 and 5) had topography consisting of ridges and troughs during low-water months, but tended to lack those features during periods of rapid water-level change (May–June, November). During these transitional periods, submerged vegetation appeared on point-bar sandbanks. Conversely, lateral sandbanks (3, 6 and 7) had at least some ridges-and-troughs year-round, and vegetation rarely or never developed on them. Lateral sandbanks had low shrimp abundance throughout the study period. When pooled across all sandbanks and dates, shrimp abundance was positively associated with presence of submerged vegetation and absence of ridge-and-trough topography (Figure 4).

Discussion

Shrimp abundance

Analysis of diel variation in shrimp abundance on Cinaruco River sandbanks revealed that the sergestid *A. paraguayensis* was present exclusively at night, whereas palaemonids, although present occasionally during daytime, were clearly more abundant during night. Nocturnal activity by palaemonid shrimp has been described for rivers in tropical (Johnson and Covich 2000; Collins et al. 2007a) and temperate (Roach and Winemiller 2011) regions. In the Cinaruco River, shrimp were more abundant during rising-water and falling-water phases when environmental conditions of sandbanks and other littoral habitats change rapidly. In rivers of the Amazon and Paraná floodplains (Walker and Ferreira 1985; Collins et al. 2007b), seasonal shrimp migration from main channel habitats to flooded areas seems to explain the

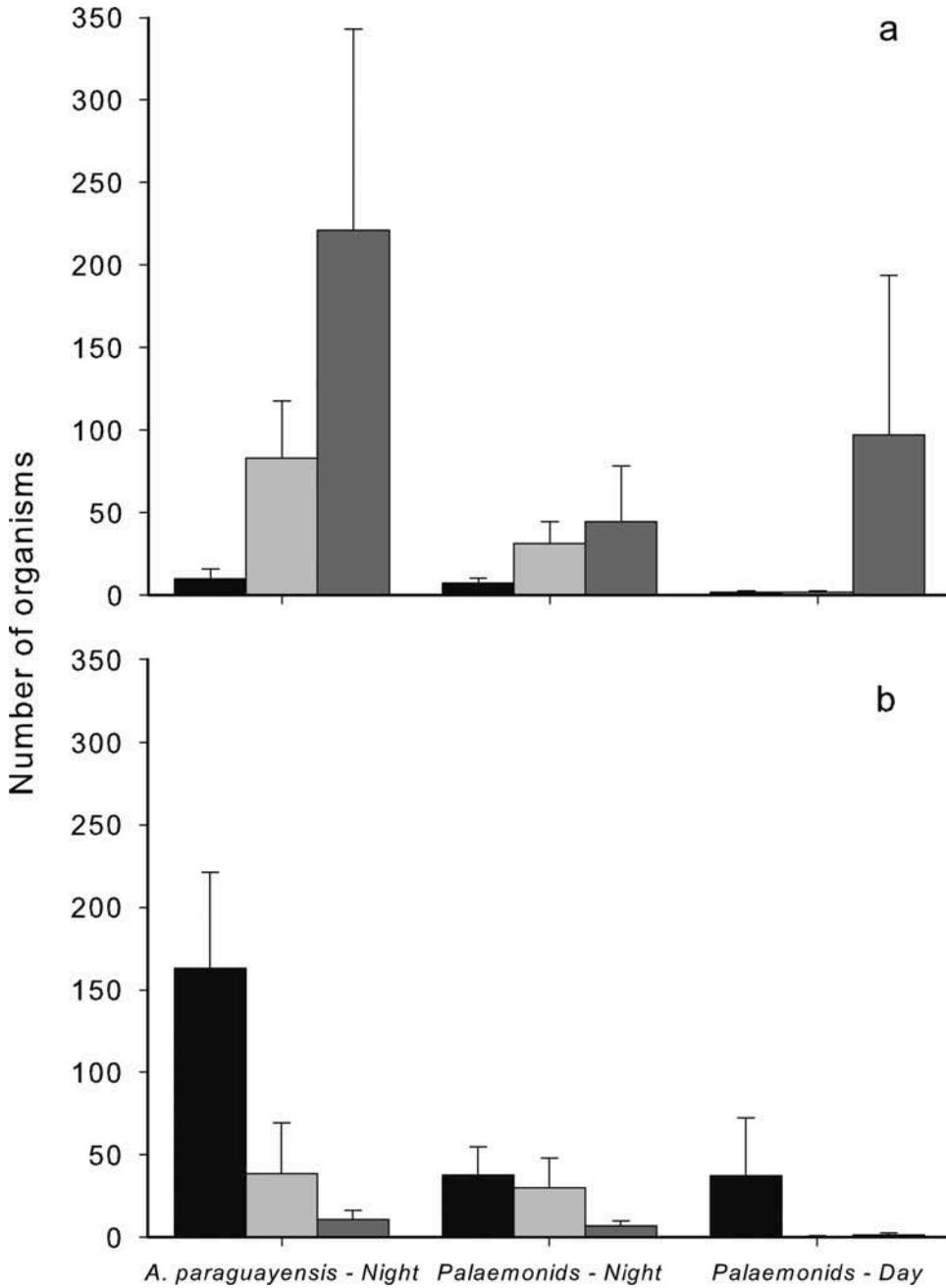Figure 4. Abundance (mean + SE) of *Acetes paraguayensis* and palaemonids during day and night for variable levels of submerged vegetation (A) and ridge-and-trough topography (B). Absent, moderate and abundant submerged vegetation and ridge-and-trough topography in the sandbanks are represented by black, light grey and dark grey bars, respectively. Plots were generated by pooling all sampling dates and sandbanks.

low numbers of shrimp in the riverbed during floods. In the present study, sampling during the high-water phase (when flooded forest and savanna are connected to the main channel) was not conducted because sandbanks were covered by several metres of water.

The ridge-and-trough topography observed on almost all sandbanks during the low-water phase was reduced or absent on many sandbanks during the periods of rising and falling water. Sandbanks 3, 6 and 7 retained this topography, yet these areas did not develop vegetation during the rising- and falling-water periods, and had low shrimp abundance. These three sandbanks were lateral banks (shallow margins of relatively straight channel reaches), whereas the other four were point bars on the inside bank of major river bends (see Figure 1). Hence, shrimp abundance on sandbanks appears to be strongly associated with fluvial geomorphology and associated local-scale environmental conditions. Submerged vegetation was present on sandbanks only during the rising- and falling-water phases, and it has never been recorded at these sites during the low-water season (February–April). The causes of seasonal appearance of submerged vegetation on sandbanks are not understood, however connections between ground water and surface water during rising- and falling-water phases might influence nutrient availability for plant growth at a patch scale (Stanford and Ward 1993; Valett et al. 1994; Brunke and Gonser 1997).

Organisms of fluvial ecosystems are adapted to exploit and survive in dynamic habitats, and the population persistence for some, if not most, of these organisms may depend upon recurrent disturbances (Humphries et al. 1999; Rempel et al. 1999; Robinson et al. 2002; Jenkins and Boulton 2003; Lytle and Poff 2004; Walks 2007; Winemiller et al. 2010). With changes in water level, organisms are forced to abandon habitat patches that become unsuitable, and colonize new ones. During the dry season, water level changes are very gradual, and there is less structural complexity in sandbank habitats. Competition and predation may become stronger in shallow littoral habitats during this period (Arrington and Winemiller 2006). Lower shrimp abundance during this period could derive from both direct (mortality) and indirect (avoidance in response to perceived threat) effects of predators. Our subsequent surveys revealed that the density of palaemonid shrimp is relatively high throughout the year in other habitats, such as leaf litter packs in littoral areas of lagoons. Hence, low numbers of shrimp on sandbanks during the dry season are probably due to the combined effects of high densities of predatory fish, absence of structurally complex refuge habitats (submerged plants), and scarcity of food resources. Troughs between ridges are inhabited by predatory fish, including diurnally active characiforms and cichlids as well as nocturnal catfish from several families (Arrington and Winemiller 2003, 2006). Several fish species common on Cinaruco sandbanks consume shrimp in addition to fish (Montaña and Winemiller 2009; Montaña et al. 2011).

Shrimp species of the Cinaruco River possess several defensive mechanisms to deter fish predation. *Pseudopalaemon amazonensis*, *Ps. chryseus*, *Ps. gouldingi* and *Palaemonetes carteri* are small and transparent and, although bottom dwellers, can swim occasionally in open water (Kensley and Walker 1982; Carvalho et al. 2006). The other palaemonid, *Macrobrachium dierythrum*, is also small and transparent but it is covered with tiny red spots that make it cryptic over the Cinaruco's orange-red sand. *Acetes paraguayensis* is small (4.5 mm cephalothorax length), transparent and swarms during diurnal migrations (e.g. some of our seine hauls contained hundreds of individuals). *Amazonsprattus scintilla*, a tiny transparent engraulid fish that inhabits

the Cinaruco River and other lowland rivers of the Orinoco and Amazon basins, also swarms in the water column in huge numbers, sometimes mixed with swarms of *A. paraguayensis* (Carvalho et al. 2006). This swarming behaviour presumably reduces per-individual encounter rates with predators.

The biology of *A. paraguayensis* is poorly documented; however, other species of the genus *Acetes* are known to form swarms of thousands of individuals that perform vertical and lateral migrations to avoid predators and to access resources on a diel basis (Xiao and Greenwood 1993). Despite intense sampling over several years, this species has not been recorded in any other habitat of the Cinaruco River other than sandbanks in the main channel at night; however, deep-water habitats were inadequately sampled, and may provide a diurnal refuge for *A. paraguayensis*. Data from the Cinaruco River are consistent with a migration pattern in which individuals occupy littoral areas during the night and migrate to open, deeper waters during the day. This migratory pattern implies that *A. paraguayensis* could provide an important trophic link between littoral and pelagic habitats (Collins and Williner 2003).

Several species of *Acetes* occupy areas near or at the bottom during daylight and move near the surface at night (Xiao and Greenwood 1992, 1993). In neritic waters, diel vertical migration in pelagic shrimp, such as *Acetes*, is believed to be synchronized with tidal currents to achieve landward transport (Omori 1974). Responses to light and tidal currents allow local populations to be maintained by a combination of horizontal and vertical movements (Xiao and Greenwood 1993). Nocturnal vertical migrations modulated by lunar cycles have been described for *Acetes intermedius* in coastal waters, finding different movement patterns depending on the moon phase (Chiou et al. 2003). Our samplings were conducted with a limited range of moon illumination and therefore they may not be able to show any relationship with the lunar phase.

It seems plausible that *A. paraguayensis* in the Cinaruco move to deep pools within the main channel during daytime. Although the main channel is assumed to have strong flow velocities, there are several riverbed forms that provide organisms with hydraulic refuges near the bottom (Kellerhals and Church 1989). In addition, major channel bends produce eddies with counter flows that create hydraulic refuges (Lagasse et al. 2004; Charlton 2008). Some knifefish (Gymnotiformes) and catfish (Siluriformes) are epibenthic inhabitants of the main channels of large Neotropical rivers with swift water currents (Lundberg et al. 1987; Barbarino Duque and Winemiller 2003). In contrast, other large aquatic vertebrates, such as turtles, crocodilians and even freshwater dolphins (*Inia geoffrensis*), tend to occupy channel areas near point sandbars on river bends instead of lateral sandbars (Smith 1993; Thorbjarnarson and Hernández 1993; Leatherwood et al. 2000; Muñoz and Thorbjarnarson 2000). Unlike point sandbars, lateral bars are not usually adjacent to deep pools. The present study suggests that *A. paraguayensis* uses point sandbanks adjacent to deep pools nocturnally because these habitats are close to deep channel areas used as refuges during daytime. Large piranhas (*Serrasalmus manueli*, *Serrasalmus rhombeus*) are abundant in deep channel areas of the Cinaruco River (pers. observation) and could induce avoidance of these habitats by fishes that are potential predators of shrimp.

Shrimp species richness

Seven shrimp species represents relatively high species richness for a single habitat within a Neotropical river. By comparison, the Caura River, an Orinoco tributary in the Guyana shield, that is four times larger than the Cinaruco, only has five shrimp species documented from extensive surveys of multiple river reaches and habitats (Magalhães and Pereira 2001). A survey conducted near the confluence of the Ventuari and Upper Orinoco rivers produced 10 shrimp species, and the investigators attributed this elevated richness to the confluence of three major biogeographical regions: Orinoco Llanos, Guyana Shield and Amazon (Pereira and García 2006).

Most of the shrimp species encountered on sandbanks of the Cinaruco River were not common. The Cinaruco is only the second reported locality within the Orinoco Basin for *Pseudopalaemon gouldingi*. An apparent undescribed *Pseudopalaemon* species was also collected in the Cinaruco. All shrimp species of the Cinaruco sandbanks are small and transparent or semi-transparent. *Macrobrachium dierythrum* is one of the smallest species in a genus with more than 200 species, and all *Pseudopalaemon* species are small. Life history traits common to the palaemonids found in this study include low fecundity, small clutch size, large eggs and reduced number of larval stages (one to three larval stages compared with 8 to 11 in other palaemonids from more productive rivers in the Orinoco Basin). This life history strategy may be adaptive when resource availability is low in unproductive aquatic ecosystems associated with the Guyana Shield (Walker 1992; Odinetz-Collard and Magalhães 1994).

The only non-palaemonid shrimp in the Cinaruco, the sergestid *A. paraguayensis*, is a poorly-known, pelagic species. Field records of *A. paraguayensis* are sporadic (Magalhães 2000), which has hindered systematic study. One or possibly two additional species of caridean shrimp are present in the Cinaruco River. A few samples taken from submerged wood in small creeks draining into Laguna Larga produced three juvenile specimens of *Euryrhynchus* sp. (Decapoda: Euryrhynchidae). This genus of small freshwater shrimp, common in black and clear water habitats within the Amazon and Orinoco basins, is often overlooked because of its tiny size and crypsis. With the additional one or two species of *Euryrhynchus*, the number of identified shrimp species for the Cinaruco increases to eight or nine, ranking it among the most species-rich rivers in South America.

Conservation implications

Information on aquatic invertebrates and the benthic ecology of tropical rivers is lacking and generally lags far behind research on fishes and limnology. Findings from the present study contribute to our understanding of the ecology of the Cinaruco River and freshwater shrimp in general. Study results indicate that a comprehensive survey of shrimp diversity would require nocturnal surveys during different phases of the annual hydrological cycle (see also Johnson and Covich 2000). Temporal and spatial patterns of shrimp abundance on sandbanks indicate strong influence of the annual hydrological regime. Shrimp were scarce during the dry season when fish densities are higher in the main channel and aquatic vegetation is absent on sandbanks. The natural flow regime is probably essential for maintaining this diverse

shrimp assemblage, not to mention the diverse fishes that number more than 280 species (Winemiller et al. 2006). Over the past decade, river ecologists have promoted the concept of the river as a network of interconnected meso-habitats (or hydraulic units) with characteristic patterns and processes that integrate across multiple scales of time and space (Palmer et al. 2000; Thomson et al. 2001; Amoros and Bornette 2002; Robinson et al. 2002; Strayer et al. 2006; Thorp et al. 2006). Because shrimp were absent or rare on sandbanks during the daytime, they clearly move among hydraulic habitat units on a diel basis. Within fluvial ecosystems, sandbanks are ubiquitous habitats that support ecosystem functions such as nutrient cycling. Although perceived to be lacking structural complexity and basal food resources, river sandbanks support diverse aquatic organisms, mostly small species of invertebrates and fish, two groups that dominate the macrofaunal diversity of tropical rivers. Given that habitat degradation is a principal cause of rapid biodiversity losses in aquatic systems worldwide (Allan and Flecker 1993; Bayley 1995; Dudgeon et al. 2006), much more research is needed to improve knowledge of benthic biodiversity and ecology in tropical rivers.

Acknowledgements

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