Linking fish colonization rates and water level change in littoral habitats of a Venezuelan floodplain river

Craig A. Layman · Carmen G. Montaña · Jacob E. Allgeier

Abstract Change in water level during the annual hydrologic cycle of tropical floodplain rivers results in continuous disassembly and reassembly of faunal communities in littoral habitat patches. As such, the rate of water level change should influence colonization rates of vagile organisms among habitat patches. We experimentally tested this hypothesis in a Venezuela floodplain river using artificial rocky patches as sampling units, water level change as the independent variable, and total number of individual fish that colonized a patch as the response variable. Water level significantly affected the total number of individuals that colonized patch habitats, i.e., rapidly receding waters were associated with higher colonization rates. Results suggest that water-level recession directly affects community assembly by influencing the rate at which individuals abandon and colonize local habitat patches.

Introduction

Many rivers are characterized by a seasonal hydrology in which water levels rise and fall somewhat gradually, yet continuously, throughout the year (Junk et al. 1989; Poff and Allan 1995; Winemiller 2004). At the landscape-scale, these events drive numerous critical ecological processes. For example, many organisms have evolved life history strategies in conjunction with the seasonal flood cycle (Arrington et al. 2006; Delong et al. 2001; Montoya et al. 2006; Winemiller 2004), and water level change is essential for nutrient cycling and energy flow from basal resource pools to secondary consumers (Lewis et al. 2000). But considered at the patch scale, seasonal water level change is a discrete disturbance to which organisms must respond (Grigg 1996; Lake 2003). For example, during water level recession, littoral patch habitats (e.g., rocky outcrops or woody snags) are exposed and dry out as waters recede. This may create a "mobility-controlled" dynamic (Townsend 1989), in which fish assemblages of littoral habitats are continuously disassembled and reassembled, on a scale of days, as organisms vacate and re-colonize patches (Arrington et al. 2005).

C. A. Layman (✉)
Marine Sciences Program, Department of Biological Sciences, Florida International University, 3000 NE 151st St., North Miami, FL 33181, USA
e-mail: laymanc@fiu.edu; cal1634@yahoo.com

C. G. Montaña
Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA

J. E. Allgeier
Odum School of Ecology, University of Georgia, Athens, GA 30602, USA

Other studies have explored some aspects of littoral patch-scale dynamics in low-lying floodplain rivers of Venezuela, e.g., demonstrating that patch size, patch type, and distance to colonization source affect local community structure (Arrington and Winemiller 2006; Arrington et al. 2005). In this study, we explicitly tested if rates of water level change influence colonization rates of vagile organisms (i.e., fish) in littoral patch habitats. We expect that more rapid water recession will force individuals to disperse at a faster rate, resulting in higher colonization rates at the patch scale (as compared to periods of more gradual water recession). In doing so, we provide new information of how an abiotic forcing variable influences among-habitat movement patterns of aquatic organisms (Albanese et al. 2004; Gilliam and Fraser 2001).

Materials and methods

The experiment was conducted in a moderate black-water floodplain river (Río La Guardia) within Venezuela's Santos Luzardo National Park, Estado Apure. Blackwater rivers in this region are characterized by low nutrients (dissolved inorganic nitrogen 0.5–2.0 μM, soluble reactive phosphorus 0.2–0.35 μM, see Montoya et al. 2006), low pH (ranging from 5 to 7), high fish diversity, sandy bottoms, and scattered floodplain lagoons. Río La Guardia has a strongly seasonal hydrology with pronounced wet and dry seasons. Like other tropical floodplain rivers, the riparian zone in Río La Guardia is flooded in the wet season (May–October) and organisms are dispersed widely throughout the inundated floodplain (Lowe-McConnell 1987; Rodríguez and Lewis 1994; Rodríguez and Lewis 1997). With the onset of the dry season (November–December), flood waters begin receding, forcing organisms off the floodplain and into the main river channel and/or lagoons (Layman et al. 2005; Layman and Winemiller 2004; Winemiller and Jepsen 1998). Small fishes in the littoral zone of the river face a high risk of predation (Layman et al. 2005; Layman and Winemiller 2004), and use physical structure, such as abundant rocks and woody snags along shorelines, as refuges (Arrington and Winemiller 2006).

Rock habitats are common along the main river channel and lagoon shorelines. We used ceramic bricks to construct simulated rock patches. The patches were constructed using 10 unglazed ceramic bricks (Fig. 1). Each brick measured 14 × 18.5 × 29 cm, and was hollow with nine internal compartments (3.5 × 5 cm) that span the longitudinal axis of the block. All blocks were arranged with the longitudinal axis positioned parallel to the direction of current flow (Arrington and Winemiller 2006; Arrington et al. 2005). Six different sampling sites along sandy beaches of the main river channel were used for this study. Approximately three times a month, from November 2004 to April 2005, a simulated rocky patch habitat was created at each site, left for 48 h, and then sampled. The same six sand banks were used each month and blocks were always placed at ∼1 m depth. Sampling occurred during daylight hours with a seine (6.4 × 1.2 m with 4 mm mesh). A 1.5 m² area containing the habitat patch was encircled with the seine, bricks were removed from inside the seine, and the seine and its contents were carefully taken ashore for removal of organisms. Because the seine completely encircled the patch, there was a low probability that organisms inside the sampling area could escape, particularly those organisms with affinities for structurally complex habitats (Willis et al. 2005). Water level depth was measured at each site before and after each experiment. For further description of the sampling protocol, see Arrington et al. (2005) and Arrington and Winemiller (2006). Data were standardized by calculating mean colonization rate/day (of the six sites) for each sampling period.

Results

A total of 574 fish representing 41 species and 11 families were sampled. As is typical of littoral habitats in lowland floodplain rivers of Venezuela, species were characterized by a wide range of morphological and ecological attributes (Arrington and Winemiller 2003; Layman et al. 2005; Layman and Winemiller 2005; Willis et al. 2005). Some of the most abundant species included pelagic characids (e.g., *Moenkhausia copei*, *Bryconops caudomaculatus*), small, insectivorous, catfishes (*Tatia concolor*, *Pimelodella* spp.), pike cichlids (*Crenicichla* af. *wallacii*), and *algivorous loricariid* catfishes (e.g., *Parotocinclus eppleyi*). More detailed descriptions of among-site and among-habitat

Fig. 1 Blocks used to simulate rocky patch habitat. The fish is a 14 cm (SL) *Platydoras* sp. catfish. Each hole in the bricks is 3×5 cm

variation of species composition in a similar floodplain river system can be found in Arrington and Winemiller (2006).

There was a significant relationship between the rate of water level recession and number of individuals that colonized a patch ($y = -0.16x + 1.6$, $F_{1,16} = 30$, $P < 0.001$, $R^2 = 0.65$) (Fig. 2a). The 48-h period with the greatest water level recession (53 cm) was associated with highest number of individuals ($n = 30$) sampled from a single patch. With this extreme data point omitted, the relationship remained significant ($y = -0.42x + 0.80$, $F_{1,15} = 54$, $P < 0.001$, $R^2 = 0.78$) (Fig. 2b). Variation in colonization rates among sites for a given sampling date was high, especially during periods of rapid water level recession.

Discussion

These data provide support for the hypothesis that rates of water level change influence colonization rates of vagile organisms to littoral patch habitats. Although this trend was robust across sites, mean colonization rates varied substantially among sites for a single sampling date. This indicates that other variables also affect colonization dynamics in these systems, including location to colonization source, ambient conditions around patches (e.g., water velocity), and landscape-scale metapopulation dynamics (Arrington and Winemiller 2006; Arrington et al. 2005). Yet despite multiple variables that likely influence colonization of
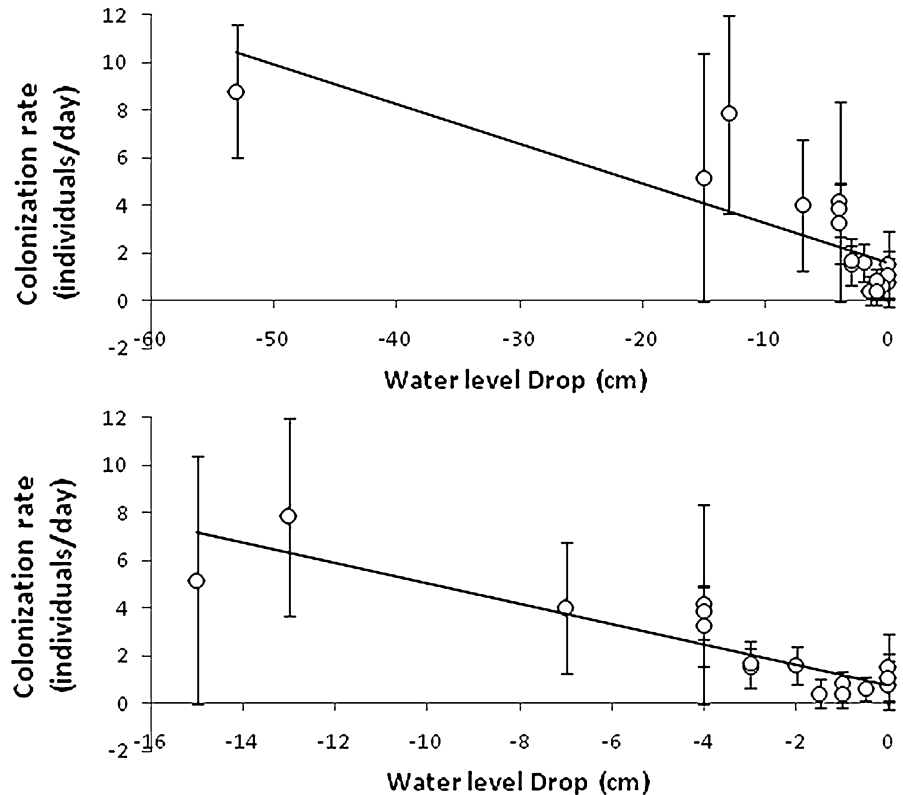
patch habitats, the rate of water level change explained 65% of the variation, implicating water level change as a primary factor driving patch colonization.

Rates of water level change, considered both *within* a single patch or *among* multiple patches, provide a framework to explore the factors that drive community assembly and dynamics in littoral habitats. *Within* habitat patch dynamics refer to the species interactions and environmental variables that may affect organisms once they colonize a patch. At this scale, during rapidly receding water periods, within-patch species interactions are likely to play a comparatively small role in determining assemblage structure. During rapidly falling water levels, equilibrium fish densities (sensu Simberloff and Wilson 1969) likely are not reached (Arrington et al. 2005), rendering species interactions less important than stochastic colonization dynamics in determining assemblage composition. During the peak dry season, however, water recession is more gradual, and species-interactions within a given patch may contribute to non-random patterns of community structure (Arrington et al. 2005).

Among patches, species interactions, especially predation, may significantly influence organism movements. With falling water levels, organisms are forced to disperse across a habitat mosaic with high densities of piscivorous fishes (Jepsen et al. 1997; Layman et al. 2005; Layman and Winemiller 2004; Layman and Winemiller 2005). Importantly, the falling water period coincides with the time when consumption rates of many predators are at an annual maximum (Arrington et al. 2006; Jepsen et al. 1997; Winemiller and Jepsen 1998; Winemiller et al. 1997), and the time when predators are most likely to affect patterns of species relative abundance (Layman et al. 2005; Rodríguez and Lewis 1994; Rodríguez and Lewis 1997). In this scenario, species-specific ability of prey to disperse, and to avoid predation, partially determines which individuals reach new patch habitats. Thus, rate of water-level recession likely alters population dynamics by influencing the rate at which individuals arrive at local habitat patches, and may indirectly alter species abundance by exposing organisms to predators.

Our study provides an example of how a key abiotic driver may affect ecological pattern and process at a local scale. Gradual and continuous water level change, a common feature of tropical floodplain

Fig. 2 Mean (±1 SD) fish colonization rates for rocky habitat patches in Río La Guardia from November 2004 to April 2005 (**a**). **b** Shows the same data without the point corresponding to the most rapid water level recession (53 cm)

rivers, creates a dynamic in which both juvenile and adult organisms are constantly forced to re-distribute across the landscape (Arrington and Winemiller 2006; Arrington et al. 2005). Results of the present study show that rate of water-level recession influences the rate at which patch habitats are colonized. Hydrologic regime is a key determinant of community structure in lotic freshwaters, and we further describe a hydrologic factor that determines local community assembly in floodplain river littoral zones.

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