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The process domains concept as a framework for fish and mussel habitat in a coastal plain river of southeastern North America

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ABSTRACT

Hydrologic processes interact with geomorphic patterns to create the spatial and temporal variation in riverine habitat that affects the distribution of aquatic species throughout stream networks. The process domains concept (PDC) states that longitudinally-abrupt changes in geomorphic processes along streams determine temporal patterns of natural disturbance that influence the distribution of stream organisms. Despite its potential generality, the PDC has been applied primarily to mountain streams of western North America. We tested the utility of the PDC as a conceptual framework for characterizing spatiotemporal variability in abiotic conditions and assessed the influence of process domains (PDs) on community composition of fishes and mussels along a fifth order river mainstem in the gulf coastal plain of the southeastern United States. We measured channel cross sections at three transects nested within three sites nested within three stream reaches to quantify multi-scale spatial variability in channel geomorphology along the mainstem of the Neches River, Texas, USA. Next, we modeled stage-dependent channel hydraulics to quantify temporal variability in habitat area and benthic disturbance. Lastly, we sampled fishes and mussels at each site and tested whether PDs correlate with spatial variation in taxonomic and functional community composition. Channel cross-sectional dimensions varied at the reach scale and affected the modeled temporal variability in habitat area and benthic disturbance. This interaction between channel geomorphology and disturbance regime indicated the presence of distinct PDs at the reach scale. Taxonomic composition of fishes did not differ among reaches, whereas abundance and richness of mussels were strongly reduced in the upper reach compared to the middle and lower reaches. Only slight differences in functional traits of fishes and mussels were apparent among reaches, suggesting that reach scale PDs do not influence community composition via the filtering of these functional traits. This study provides empirical evidence that the PDC is a useful framework for describing hydrogeomorphic conditions and mussel abundance and richness and can guide channel restorations in streams draining regions of low topography.

1. Introduction

Aquatic ecologists have long recognized that spatial and temporal variability in abiotic conditions are important determinants of fish and mussel community composition in streams and rivers throughout the world (Gorman and Karr, 1978; Schlosser, 1987; Strayer, 1993; Townsend and Hildrew, 1994; Grossman et al., 1998). A variety of conceptual frameworks have been developed and empirically tested over the years and have advanced understanding of lotic ecology. These frameworks have also demonstrated the mechanistic connections between physical sciences (*e.g.*, fluvial geomorphology) and biological sciences (*e.g.*, stream ecology) and provide a foundation for designing stream and river restoration projects (Poole, 2010). The river continuum concept (RCC) is a conceptual framework linking gradual shifts in channel geomorphology and resource origin with concomitant shifts in macroinvertebrate and fish community composition from headwaters to large rivers (Vannote et al., 1980). Montgomery (1999) proposed the process domains concept (PDC) as a complementary conceptual framework to the RCC. The PDC posits that spatial variability in geomorphic processes determines temporal patterns of natural disturbance that influence the population dynamics and distribution of stream organisms. In contrast to gradual changes described by the RCC, the PDC divides stream networks into discrete zones (*i.e.*, process domains (PDs))

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distinguished from one another by different geomorphic processes and natural disturbance regimes. For example, stream reaches bounded by canyons are likely to experience landslides as disturbances, whereas reaches in open floodplains are subject to disturbances related to channel migration (Montgomery, 1999). Despite its potential generality to understanding spatiotemporal variability in stream habitat around the world, the PDC has been applied primarily to mountain streams of western North America where the concept was developed (*e.g.*,Baxter and Hauer, 2000; Ebersole et al., 2003; Buffington et al., 2004). Empirical tests of the PDC in river systems from a variety of ecoregions are necessary to evaluate the PDC as a broadly-applicable framework for understanding abiotic drivers of stream community composition. Such tests will also inform ecological engineers tasked with designing and restoring stream channels that re-establish natural geomorphic processes and ecological integrity (Rosgen, 1996; Pedersen et al., 2007; Palmer et al., 2005).

Distributions of species are linked to environmental conditions through their functional traits (McGill et al., 2006). Understanding trait–environment relationships is necessary to predict species' responses to anthropogenic environmental change (Poff and Allan, 1995). Among stream fish species, morphological traits determine affinities for different mesohabitat types (*i.e.*, pool, riffle, run) (Lamouroux et al., 2002). Tradeoffs among key life history traits (*i.e.*, age at maturity, fecundity, and parental investment per progeny) result in three strategic endpoints (*i.e.*, equilibrium, opportunistic, and periodic) among freshwater fish species (Winemiller and Rose, 1992). In lotic habitats, these life history strategies are filtered by several aspects of the hydrologic regime including interannual variability, predictability, and timing of high- and low-discharge events (Mims and Olden, 2012). These flow regime components vary along the river continuum as well as between regulated and unregulated rivers. Trophic traits also influence the distribution of fish species along the river continuum (Poff and Allan, 1995; Ibanez et al., 2009) as well as between pool and riffle mesohabitats (Lamouroux et al., 2002).

The distributions of freshwater mussel species also are linked to the environment via the filtering of functional traits. Abiotic environmental conditions mediate spatial distributions of freshwater mussels. Tradeoffs among life history traits (*i.e.*, body size, size at maturity, growth rate, fecundity, brooding duration, and glochidia size) represent divergent life history strategies (*i.e.*, equilibrium, opportunistic, and periodic) that are filtered by components of the hydrologic regime representing variability and predictability of high- and low-discharge events (Haag, 2012; Daniel and Brown, 2014). Vaughn (2012) used a metapopulation framework to show that brooding duration (*i.e.*, short- *versus* long-term brooding) influences extinction rates of local populations. Mussels also vary in valve shape and disk sculpturing which has been shown to vary along the river continuum, possibly in response to increasing hydraulic stress downstream (Savazzi and Peiyi, 1992; Watters, 1994; Hornbach et al., 2010). Thermal tolerance can influence the distribution of mussels in streams that cease to flow during the summer and surpass upper thermal limits of thermally-intolerant species (Spooner and Vaughn, 2008). Gradients of anthropogenic disturbance such as land use in adjacent and upstream riparian corridors and upstream catchments affect water quality and in-stream habitat (Allan, 2004) and frequently affect mussel abundance and species distributions (Strayer, 1983; Atkinson et al., 2012). Biotic components of the environment also mediate spatial distributions of freshwater mussels via the filtering of functional traits associated with fish host infection. For example, Haag and Warren (1998) demonstrated that host generalists, host specialists with attraction, and host specialists without attraction correlate with fish communities that vary along the river continuum. Host infection strategy has also been shown to influence colonization rates of mussels in streams of southeastern Oklahoma (Vaughn, 2012). Many of these abiotic and biotic conditions vary with longitudinal stream network position causing changes in community composition along the river continuum. Because PDs vary in discharge-related disturbance regime, organic matter retention, and mesohabitat characteristics (Montgomery, 1999), variation in fish and mussel community composition among PDs may be determined by functional traits associated with resource acquisition, tolerance to abiotic stressors, life history, or colonization and extinction rates.

1.1. Study objectives and hypotheses

In this study, we evaluate the PDC as a conceptual framework for understanding spatiotemporal variability in abiotic conditions along a fifth order river mainstem in the gulf coastal plain of southeastern North America. Specifically, we identify the spatial scale at which systematic changes in channel geomorphology are apparent and use hydraulic modeling to quantify the flow-related disturbance regime and temporal variability in habitat area with the objective of identifying distinct PDs in the upper Neches River, Texas, USA. We then use taxonomic and functional (*i.e.*, trait-based) approaches to test PDs as drivers of fish and mussel community composition along this river mainstem. We hypothesized that PDs with more frequent and severe disturbances would filter functional traits of both fishes and mussels. First, we hypothesized that fish species with opportunistic life history strategies and omnivorous trophic classifications would persist in or be able to rapidly colonize these PDs following flow-related disturbances (Poff and Allan, 1995). Second, opportunistic mussel species that exhibit short life spans, early maturation, and high fecundity should be more resistant to benthic disturbances and more likely to recolonize following disturbances, allowing these species to persist in these PDs (Haag, 2012). Third, mussel species with morphological adaptations (disk sculpturing and/or valve shapes with low centers of gravity) to withstand dislodgement should persist in PDs with frequent and severe benthic disturbances (Savazzi and Peiyi, 1992; Watters, 1994).

2. Materials and methods

2.1. Study area

The Neches River flows from its headwaters in northeastern Texas, southerly to the Gulf of Mexico in southeastern Texas (Fig. 1). The upper basin drains the South Central Plains EPA Level III ecoregion and land cover is 35.3% pasture or hay, 23.2% forest, 12.4% wetland, 10.9% urban, 8.9% shrubland, 5.6% open water, and 3.7% cultivated (Vogelmann et al., 2001). The upper basin has one mainstem impoundment, Lake Palestine, which was constructed for municipal water supply and recreation. Discharge from the Lake Palestine dam averages 4.0 $m^3 s^{-1}$ with larger releases in the winter and spring. The study took place in the upper mainstem beginning at the Lake Palestine dam where it is a fifth order stream draining 2138 km^2 and ending 128 river km downstream where it remains a fifth order stream and drains 4153 km^2. Eight small tributary confluences are distributed uniformly along the Neches River mainstem within the study area and gradually contribute discharge (Fig. 1).

We used a nested sampling design to evaluate the spatial scale at which channel geomorphology, temporal variability in habitat area and hydraulics, and fish and mussel community composition varied. We sampled fishes and mussels and surveyed channel geomorphology at three transects, nested within three sites (400 m in length), which were nested within three geomorphically distinct