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Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position

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Abstract I tested the effects of pool size and spatial position (upstream or downstream) on fish assemblage attributes in isolated and connected pools in an upland Oklahoma stream, United States. I hypothesized that there would be fundamental differences between assemblages in these two pool types due to the presence or absence of colonization opportunities. Analyses were carried out at three ecological scales: (1) the species richness of pool assemblages, (2) the species composition of pool assemblages, and (3) the responses of individual species. There were significant species-volume relationships for isolated and connected pools. However, the relationship was weaker and there were fewer species, on average, in isolated pools. For both pool types, species incidences were significantly nested such that species-poor pools tended to be subsets of species-rich pools, a common pattern that ultimately results from species-specific differences in colonization ability and/or extinction susceptibility. To examine the potential importance of these two processes in nestedness patterns in both pool types, I made the following two assumptions: (1) probability of extinction should decline with increasing pool size, and (2) probability of immigration should decline in an upstream direction (increasing isolation). When ordered by pool volume, only isolated pools were significantly nested suggesting that these assemblages were extinction-driven. When ordered by spatial position, only connected pools were significantly nested (more species downstream) suggesting that differences in species-specific dispersal abilities were important in structuring these assemblages. At the individual-species level, volume was a significant predictor of occurrence for three species in isolated pools. In connected pools, two species showed significant position effects, one species showed a pool volume effect, and one

species showed pool volume and position effects. These results demonstrate that pool size and position within a watershed are important determinants of fish species assemblage structure, but their importance varies with the colonization potential of the pools. Isolated pool assemblages are similar to the presumed relaxed faunas of montane forest fragments and land bridge islands, but at much smaller space and time scales.

Key words Colonization · Extinction · Nestedness · Species-volume relationship · Stream fishes

Introduction

Species within a community may differ greatly with respect to their dispersal abilities and the spatial scale required to carry out their life histories (Wiens 1989). These considerations are especially critical in insular systems. The size and degree of isolation of an island (or habitat patch) may interact with species-specific differences in life history traits, leading to variation among species in immigration ability and extinction susceptibility, both of which influence the species composition of local communities (Lomolino 1986; Cutler 1991; Kadmon 1995).

One common pattern that results from such differences among species is that of nested subsets. A nested community pattern occurs when assemblages of different numbers of species form nested subsets of one another (Patterson and Atmar 1986). Ultimately, nestedness results from differences among species in immigration ability or susceptibility to extinction (Patterson and Atmar 1986). The prevalence of nestedness across a wide variety of taxa and geographic regions suggests that it may be a general ecological property with applicability to continental and true island communities (Patterson 1990; Patterson and Brown 1991).

In this study I examined the importance of pool size and spatial position (upstream or downstream) on fish assemblage attributes in isolated and connected (flow-

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through) pools in a small, upland stream. Isolated pools had no colonization opportunity, while connected pools were connected to upstream and downstream habitats. Individual stream pools are discrete habitat units for fishes and thus represent an appropriate scale for studying factors that influence the richness and composition of stream fish assemblages (Angermeier and Schlosser 1989; Capone and Kushlan 1991; Matthews et al. 1994).

The importance of pool size and spatial position were evaluated at three ecological scales: (1) species richness of pool assemblages, (2) composition of pool assemblages, thus maintaining species' identities, and (3) species-level responses. The following two assumptions were made.

1. The probability of immigration should decline in an upstream direction due to distance (isolation) effects. This idea is supported by the literature on stream fishes (Sheldon 1967; Schlosser 1987; Osborne and Wiley 1992) and is predicted based on island biogeography theory (MacArthur and Wilson 1967). Given the hierarchical nature of stream networks and the constant downstream movement of materials, recolonization after disturbance (e.g., floods) often must come from downstream "refuge" habitats (see Ward and Blaustein 1994).
2. The probability of extinction increases as habitat size decreases. Larger islands support larger populations which are less vulnerable to extinction (MacArthur and Wilson 1967). Large stream habitats provide more refugia, greater habitat complexity, and more living space (Schlosser 1987), thus ameliorating local extinction, while smaller habitats are more environmentally variable and less persistent (Capone and Kushlan 1991).

Methods

Study area and species

Cucumber Creek is a third-order, upland stream in the Mountain Fork drainage of the Little River system, Leflore County, Oklahoma, United States. The watershed is in the Ouachita Biotic District (Blair and Hubbell 1938) and is characterized by strongly folded sedimentary rock and pine-oak upland forest. The stream channel is strongly braided throughout much of its length. During the summer surface flows cease in numerous places throughout the watershed, especially in secondary channels, forming isolated pools of various sizes.

Twelve species of fishes, taxonomically distributed across five families, were found in Cucumber Creek stream pools. Functionally, these fishes occupy several different roles in their environment. The following functional descriptions of these species are adapted from the criteria of Allan (1995) and Poff and Allan (1995), while the descriptions of regional distribution patterns are derived from Miller and Robison (1973), Rutherford et al. (1992), and Taylor and Lienesch (1996a,b).

Esox americanus (grass pickerel) and *Micropterus dolomieu* (smallmouth bass) are primarily piscivores and attain their greatest abundances lower in the drainage system; the former in vegetated lowland streams and the latter in larger streams. The sunfishes

Lepomis megalotis (longear sunfish), *L. macrochirus* (bluegill), and *L. cyanellus* (green sunfish) are best described as generalized invertebrate feeders that feed opportunistically at all depths. *L. megalotis* and *L. cyanellus* are both common inhabitants of small upland streams in the region, while *L. macrochirus* is mostly encountered in lentic habitats that are usually associated with larger and more lowland streams in the drainage. *Etheostoma radiosum* (orangebelly darter) and *Erimyzon oblongus* (creek chubsucker) are benthic invertebrate feeders; both are common inhabitants of small upland streams in the region. The cyprinids (minnows) occupy four different trophic roles including an herbivore *Campostoma anomalum* (stoneroller), the surface and water column feeders, *Lythrurus snelsoni* (Ouachita Mountain shiner) and *Notropis boops* (bigeye shiner), the omnivore *Pimephales notatus* (bluntnose minnow) and the generalized invertebrate feeder *Semotilus atromaculatus* (creek chub). All of these species are common in the upper Mountain Fork drainage. The catfish *Ameiurus natalis* (yellow bullhead) is also omnivorous and is widespread throughout the drainage. *Etheostoma radiosum* and *L. snelsoni* are endemic species in the Red River drainage; *L. snelsoni* is further limited to the Little River system (Taylor and Lienesch 1996a,b). Although overlap in functional designation occurs (i.e., large, adult *S. atromaculatus* will readily consume fishes), these categories serve to illustrate the predominant trophic roles of these species and the functional variety found within this taxonomic assemblage. All species, their taxonomic affiliations, and their summarized ecological attributes are given in Table 1.

Data

I quantified fish assemblages in 30 pools in Cucumber Creek from 27 June 1994 to 22 July 1994. Pools were scattered throughout an 11-km reach of the stream; 15 pools were isolated and no surface flows entered or exited the pool habitats, while the remaining 15 pools were flow-through, bounded above and below by riffle habitats that were connected to other pool habitats.

Each pool was surveyed by entering the pool at the downstream end and snorkeling through the entire pool while observing and recording all fish species that were present. This sampling method was very efficient in this instance due to the clear waters of Cucumber Creek. For each pool, transects (perpendicular to the stream's course) were placed at 5- to 10-m intervals depending on pool size. At every other meter along transects depth and dominant substrate type were measured. Substrate was categorized according to Taylor and Lienesch (1996a,b) as bedrock, large boulder (> 300 mm), small boulder (150–300 mm), cobble (50–149 mm), gravel (3–49 mm), or sand (< 3 mm). Maximum current speed (in flowing pools) and stream width were measured on each transect and the presence/absence of aquatic macrophytes, filamentous algae, undercuts, and woody debris was also recorded for each transect.

I calculated mean stream widths and depths for each pool. Each substrate category occurring in a pool was represented as the percentage of the total number of substrate point-estimates. Substrate diversity was calculated for each pool using the Shannon-Wiener diversity index. Undercuts, aquatic macrophytes, filamentous algae, and woody debris were represented as the percentage of transects where present for each pool. Pool volumes were calculated by multiplying mean width, mean depth, and length. For all analyses, pool volumes were \log_{10} -transformed. Pool distances upstream from the confluence with a much larger stream (at the downstream end of the study area) were transformed to ranks.

Analyses

Correlation and multiple regression were used to determine how well pool volume, distance upstream (hereafter called distance), and substrate diversity could predict pool richness for isolated and connected pool data sets. Whether species richness differed between pools with and without woody debris, for each pool type, was

Table 1 Taxonomic affiliations, mean volume and range, and median distance (rank distance upstream) and range for all observed species in connected and isolated stream pools

Taxonomy	Connected pools				<i>n</i>	Isolated pools				<i>n</i>
	Volume		Distance			Volume		Distance		
	Mean	Range	Median	Range		Mean	Range	Median	Range	
Esocidae										
<i>Esox americanus</i>						6.5		12.0		1
Cyprinidae										
<i>Campostoma anomalum</i>	40.6	1.5–140.6	10.0	1–29	15	37.3	1.2–140.6	18.0	3–27	9
<i>Lythrurus snelsoni</i>	54.6	4.5–140.6	9.5	1–16	8	13.2	1.2–32.5	22.5	3–27	8
<i>Notropis boops</i>	40.6	1.5–140.6	10.0	1–29	15	31.5	1.2–140.6	20.0	3–27	9
<i>Pimephales notatus</i>	102.8		10.0		1					
<i>Semotilus atromaculatus</i>	31.8	1.5–140.6	14.0	5–29	11	27.3	1.2–102.8	20.5	3–30	12
Catostomidae										
<i>Erimyzon oblongus</i>	40.6	2.5–140.6	13.0	1–28	11	32.6	1.5–140.6	20.0	8–27	11
Ictaluridae										
<i>Ameiurus natalis</i>						71.4	1.5–140.6	17.0	11–18	3
Centrarchidae										
<i>Lepomis megalotis</i>	55.4	6.5–140.6	14.0	1–29	7	21.3	6.5–56.4	19.0	8–27	4
<i>L. macrochirus</i>						8.7		27.0	3–30	1
<i>L. cyanellus</i>	102.8		10.0		1	12.0	6.5–19.0	25.0	12–27	4
<i>Micropterus dolomieu</i>	63.1	4.5–119.1	4.0	1–10	5	1.2		3.0		1
Percidae										
<i>Etheostoma radiosum</i>	31.7	1.5–119.1	10.0	1–29	13	27.0	1.2–140.6	23	3–30	8

tested with analysis of variance. Other measured habitat variables were of low frequency and were not statistically analyzed. The *T* of Atmar and Patterson (1993) was used to determine the degree of nestedness in each data set. This metric measures the unexpected presences and absences on islands that have been “packed” into a state of maximum nestedness. A Monte Carlo procedure (Atmar and Patterson 1995) was used to assess the probability that such a distribution pattern could occur by chance. To investigate the potential roles of immigration and extinction in leading to nested patterns, I ordered pools in both pool-by-species data matrices by distance and pool volume and used a Monte Carlo randomization procedure developed by Lomolino (1996) to test whether nestedness was associated with pool volume or distance. Finally I examined the effects of pool volume and distance upstream on individual species distributions using a methodology described by Lomolino (1986). For each species that had at least 3 and not more than 12 occurrences in a data set, discriminant analysis was used to discriminate between pools where the species was present vs absent based on distance and pool volume. For each discriminant model, variables were retained only if they were significant at $P \leq 0.05$.

Results

Multiple regression analyses indicated that only volume was a significant predictor of species richness in both pool types (Table 2). Pool volume, distance, and substrate diversity showed weak and insignificant patterns of covariation with each other, so multicollinearity was not a problem in the multiple regression models. Analysis of variance indicated that the presence of woody habitat structure in pools had no effect on species richness for either pool type ($P > 0.05$, both pool types). The species-volume slope (*z*-score) was higher for iso-

lated pools than for connected pools (Table 3; Fig. 1), though analysis of covariance indicated no statistical difference. However, adjusted means (after dropping the interaction term) were significantly different such that

Table 2 Results from multiple regression of log species richness onto log pool volume, rank distance upstream, and substrate diversity; $n = 15$ for both pool types. Standardized coefficients give the relative influence of each variable in the regression model, *P* values indicate the significance of each variable, and R^2 gives the variance accounted for in the overall model

Pool type	Variable	Standardized coefficient	<i>P</i>	R^2
Connected	Volume	0.78	0.001	0.65
	Distance	−0.23	0.242	
	Substrate diversity	0.15	0.459	
Isolated	Volume	0.52	0.048	0.58
	Distance	−0.33	0.197	
	Substrate diversity	0.34	0.188	

Table 3 *Y*-intercepts, slopes, coefficients of determination (R^2), and significance levels (*P*) for connected and isolated pools; $n = 15$ for both pool types

Pool type	Intercept	Slope	R^2	<i>P</i>
Connected	0.63	0.12	0.56	0.001
Isolated	0.41	0.17	0.27	0.047

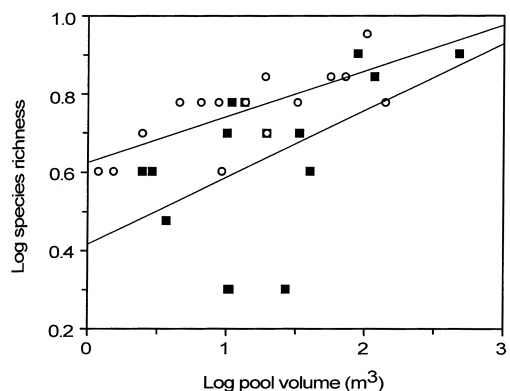


Fig. 1 Log species richness against log pool volume for connected (circles) and isolated (squares) pools

more species occurred, on average, in the connected pools than in the isolated pools ($F = 8.20$, $P = 0.008$; Fig. 1).

Both types of pools showed significant patterns of nestedness (connected, $T = 18.18^\circ$, $P < 0.001$; isolated, $T = 28.2^\circ$, $P < 0.001$). However, when ordered by volume and isolation, fundamental differences were found between the two data sets. Connected pools were significantly nested when ordered by distance upstream ($P = 0.049$), while temporary pools were significantly nested when ordered by pool volume ($P = 0.006$).

Occurrences of 5 of the 13 species inhabiting the watershed exhibited significant responses to pool volume and/or distance (Fig. 2). For isolated pools, *Lepomis megalotis* (longear sunfish), *Semotilus atromaculatus* (creek chub), and *L. cyanellus* (green sunfish) showed significant responses to pool volume. For connected pools, *L. megalotis* was associated with pool volume, while *S. atromaculatus* and *Micropterus dolomieu* (smallmouth bass) both showed distance effects. *L. snelsoni* was the only species to show both distance and volume effects.

Discussion

In ecological time, community diversity is a balance between local biotic and abiotic factors, which tend to reduce local diversity, and dispersal from the surrounding region, which can augment local diversity. An appropriate scale for investigating these local and regional effects is one where the assemblages of interest are all connected by dispersal, thus forming a “metacommunity” (Ricklefs and Schluter 1993). This mesoscale (Roughgarden et al. 1988) view of a system lies in between the local-scale mechanisms that concern community ecologists and the large-scale processes that engage biogeographers and systematists (Holt 1993).

In streams, additive patterns of fish species richness along a downstream continuum are common (Sheldon 1967; Rahel and Hubert 1991). There is uncertainty about the mechanisms leading to this pattern, but it is

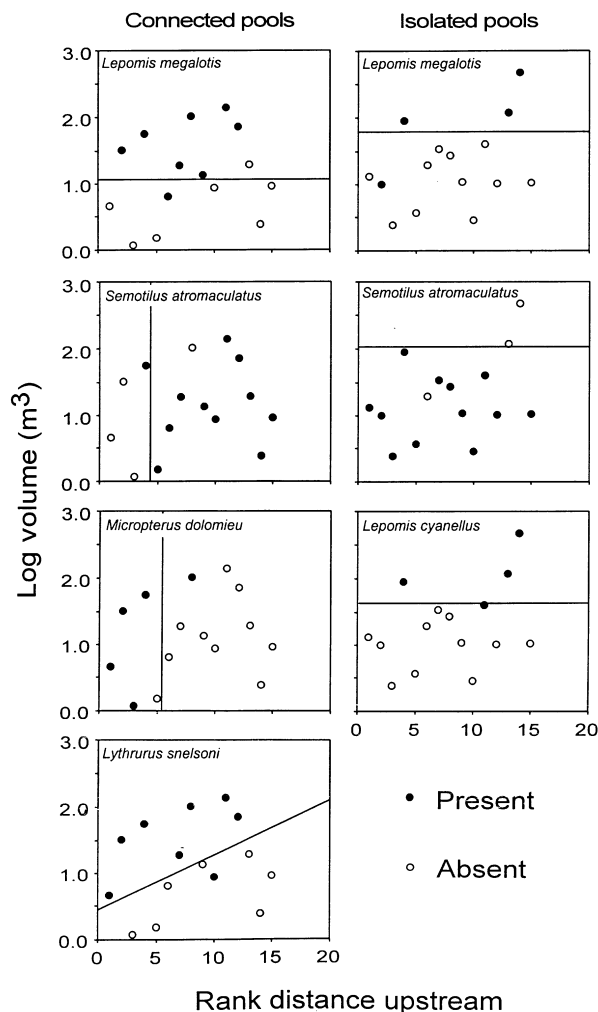


Fig. 2 Three-dimensional presence/absence diagrams for species in connected and isolated pools. Filled and open circles represent presence/absence in individual pools, respectively, plotted as a function of log pool volume and rank distance upstream. Lines indicate significant ($P < 0.05$) responses of species to distance (vertical), pool volume (horizontal), and both variables (diagonal)

apparent that in many stream systems, if the spatial scale is appropriate to incorporate sufficient environmental variability, downstream habitats tend to have better pool development, higher habitat diversity, greater environmental stability, and more diverse fish assemblages than headwater habitats (Schlosser 1987). In this investigation, pool volume and distance upstream were uncorrelated. Pools of various sizes were interspersed throughout the stream reach for both pool types. Pool volume was the most important factor predicting the number of coexisting species in both pool types, independent of distance upstream and substrate diversity. Maximum and mean depth were both strongly correlated with pool volume. Greater depth can provide fishes with a refuge from terrestrial predators (Power 1984). Furthermore, Gorman (1988a) showed, in a small upland Missouri stream, that fishes finely partitioned this vertical component of stream habitat, and that segre-

gation was due to a combination of habitat selection modified by interspecific interactions (Gorman 1988b).

Because of the differences in colonization potential between these two pool types, I expected differences in species-volume relationships. According to island biogeography theory, I anticipated that the slopes of the two regression lines would differ. In isolated pools, extinction should be more severe in smaller pools, while for connected pools of all sizes, populations may be sustained by immigration from adjacent habitats (i.e., rescue effect; Brown and Kodric-Brown 1977). If this is true, the resulting species-volume curve should be steeper for isolated pools than connected pools. A potential problem arises when comparing data sets with different island (or patch) size-ranges because the slope of the species-area (or volume) relationship is dependent upon variation in the independent variable (Martin 1981).

In this study, isolated and connected pools had volumes with different ranges. One isolated pool was larger than any connected pool and two connected pools were smaller than any isolated pool. Regardless of these differences, the slopes of the two relationships did not differ significantly. However, there was a significant difference between connected pools and isolated pools with respect to species richness. With colonization lacking, extinction apparently took its toll on the isolated assemblages. Isolated pools showed considerably more scatter around the regression line than did connected pools (Fig. 1).

Because colonization of isolated pools was not a possibility within the timespan of this study, the large amount of variability present (compared to connected pools) must have been due to irregularity in local extinctions. The source of this variation may have been, in part, due to the differential in time since pool isolation. In other words, as flow rates declined, pools were not likely to have all been isolated from the main channel at the same time.

As with the species-volume relationships, patterns of nestedness were strikingly different depending on whether colonization opportunities were possible. Both pool types were significantly nested such that species-poor pools tended to be subsets of more speciose pools. This nonrandom pattern of species incidences is common in nature (Wright and Reeves 1992; Cook and Quinn 1995) but reveals little about the causality of nestedness. Previous studies have emphasized the importance of extinction in producing nested community patterns (see Cook and Quinn 1995). Systems thought to be largely influenced by colonization (e.g., oceanic archipelagoes) were often found to be poorly nested. However, lack of nested patterns in such systems is not surprising due to the confounding effects of other biogeographic processes operating simultaneously, such as local population differentiation and speciation. There is evidence suggesting that frequent colonization can enhance nestedness. Cook and Quinn (1995), using more than 50 published island biogeographic data sets, found that superior dispersers tended to show a higher degree of nestedness than poorer dispersers, a result opposite of

what would be expected if colonization were less deterministic than extinction. However, these results must be interpreted cautiously for the same reasons that nested subsets appear to be lacking on many oceanic archipelagoes: any amount of differentiation among populations will tend to enhance beta-diversity and act against a nested subset pattern (Wright and Reeves 1992). Even though Cook and Quinn (1995) excluded endemic species from their analyses, poor dispersers on an archipelago will undergo greater population differentiation than strong dispersers due to isolation effects on gene flow. Without estimates of gene flow or data concerning species' resource utilization patterns, the contention that land-bridge islands should, a priori, exhibit stronger nestedness patterns than oceanic islands is not compelling, in and of itself.

Nestedness in aquatic systems excluding parasite communities has only recently been investigated. Kodric-Brown and Brown (1993) found that isolated springs in Australia had highly nested fish assemblages and Vaughn (in press) found that freshwater mussel faunas in 13 of 14 eastern United States rivers were significantly nested. In both of these studies, the authors speculated on the importance of extinction events in producing nested patterns. The stream pool data presented here provide a unique opportunity to assess the relative importance of colonization and extinction in producing nested subset patterns. Assuming that variation in pool volume and position within the watershed interact with species-specific life history traits, and that such interaction can lead to differential extinction and immigration among species, it should be possible to test for the importance of immigration and extinction in leading to nested assemblage patterns. When both pool types were ordered by volume and distance upstream, nestedness was significantly associated with volume for isolated pools, while for connected pools, nestedness was associated with distance upstream. This is consistent with the idea that extinction, which should vary with pool size, largely determines the composition of isolated pools, while in connected pools, species occurrence patterns appear to be influenced by differences in dispersal ability among species. Thus, volume largely explains the number of coexisting species in both isolated and connected stream pools, but the composition of pool assemblages also differs depending on colonization potential. Assemblages in isolated pools appear to be extinction-driven. In contrast, assemblages within connected pools appear to be influenced, at least in part, by differential immigration abilities among species.

Although differential immigration appears to contribute to nestedness patterns in connected stream pools, the effects of pool volume cannot be discounted. Consider the following scenario: if all connected pools were of identical size and quality and were nested, the pattern generating mechanism would be the gradient in species' dispersal abilities. Extinction rates would be high in upstream pools, while rescue effects would buffer extinction in downstream pools. Whether or not this fil-

tering effect acting alone could maintain a nested pattern is questionable. Now consider pool volume as a second variable. In this modified scenario, we would expect a population-size dependent filtering effect to occur as it did for the isolated pool assemblages, but operating in conjunction with the dispersal gradient. Both conditions are now important and will affect a species' persistence time in a given pool. The important question is whether the interactive effect of both processes occurring together will disrupt species ordering and thus, nestedness. In this data set, the two mechanisms appear to interact in such a way as to increase nestedness; the matrix temperature of the connected pools was 10° lower than that of the isolated pools. Whether this difference is ecologically meaningful is unknown; the point is that the two processes together did not disrupt the nested pattern. As with the species-volume relationships, the higher matrix temperature (less order) of the isolated pools may, in part, be due to the differential in length of time since pool isolation.

The potential importance of immigrations and extinctions on stream pool assemblages can also be examined from the perspective of individual species' occurrences. In the extinction-driven isolated assemblages, individual species should be associated with pool volume rather than distance upstream. In connected pools, a different pattern is to be expected; species occurrences should depend on (1) the ability to disperse in an upstream direction, and (2) the ability to maintain a minimum sustainable population in a given pool.

In isolated pools, three species showed significant associations, all with pool volume (Fig. 2). For connected pools there was more variability in species' responses. Two of the four species with significant associations showed only distance effects, one species showed a volume effect, and one species showed distance and volume effects. Thus, these species-level responses are largely consistent with predictions that resulted from the assemblage-level analyses.

Species distributional patterns emerged from the species-level analyses that are of interest. In isolated pools, *L. megalotis* and *L. cyanellus* both tended to occur in large pools, while *S. atromaculatus* was mostly found in small pools. In connected pools, *S. atromaculatus* mostly occurred in upstream pools, while *M. dolomieu* most often was found in downstream pools. *S. atromaculatus* is widely known to occur in small stream habitats across its geographic range (Lee and Platania 1980; Miller and Robison 1973; Robison and Buchanan 1988). In Cucumber Creek stream pools, this species showed opposite responses depending on pool type (Fig. 2). Furthermore, in both pool types, its response was opposite to that of both *Lepomis* spp. (isolated pools) and *M. dolomieu* (connected pools)(Fig. 2), suggesting that interactions among species may also have affected species' distribution patterns at the meso-scale. These patterns are characteristic of niche partitioning and competitive exclusion, processes which will tend to counteract filtering mechanisms that promote

nestedness. Each of the above species are potential competitors for space and food to varying degrees.

The results presented here are largely consistent with those from systems that operate on much larger space and time scales. For example, the faunas of land-bridge islands and isolated mountaintops are generally very strongly nested (Patterson and Atmar 1986; Wright and Reeves 1992) and are thought to be structured largely by extinction rather than immigration. Although colonization may be more important than previously realized in many of these systems (Lomolino et al. 1989; Cook and Quinn 1995), it seems apparent that selective extinction often plays a critical role in structuring these large-scale faunas. However, unlike these large-scale relaxation faunas, extinction as well as colonization appear to be important determinants of Cucumber Creek fish assemblages. Other evidence suggests the near-deterministic nature of colonization in streams (Matthews 1986; Meffe and Sheldon 1990; Peterson and Bayley 1993). These studies (both manipulative and observational) have shown that stream fish assemblages tend to return to their pre-disturbance structure if colonization opportunities and habitat structure are left intact. While the results presented here suggest a highly determined nature to the processes of colonization and extinction in this stream system, the question of the assemblage's stability with regard to species-volume, nestedness, and species' occurrence patterns over a significant period of time remains to be ascertained.

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