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Spatio-temporal patterns of fish assemblage structure in a coastal plain stream: appropriate scales reveal historic tales

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Abstract – Quantifying assemblage structure across spatio-temporal scales is ecologically important and further aids in the understanding of community organisation processes. Currently, few studies have assessed assemblage structure across generous magnitudes of scale, and influences of processes (biotic and abiotic) responsible for structuring assemblages are still questioned. Using community and hydrologic data collected over a 22-year period from a stretch of river nearing 150 km, we examined spatio-temporal fish assemblage structural patterns in a temperate coastal plain stream. Results indicated that significant changes in assemblage structure across time were influenced by environmental disturbances, including drought and hurricane events. Assemblages were restructured in a punctuated manner directly following these events, and complete recovery of initial assemblage structure did not occur across the study period. Additionally, we found spatial differentiations between upstream and downstream assemblages, which were driven by greater abundances of several species in downstream sites. Our results suggest that assemblage structure is influenced by environmental variation, specifically, extreme disturbance events and spatial habitat heterogeneity.

Key words: Pearl River; community ecology; community structure; fishes; hurricane

Introduction

The evaluation of assemblage structure across spatio-temporal scales is paramount towards a better understanding of species composition in ecological communities. Moreover, quantifying structural patterns can aid in recognising and further understanding underlying processes active in regulating assemblage structure (i.e., biotic and abiotic processes). Studies examining fish assemblage structure across time and space have been numerous (e.g., Moyle & Vondracek 1985; Ross et al. 1985; Johnston & Maceina 2009), but despite the vast amount of work on this theme, the adequacy of spatial and temporal scales used has often been questioned (e.g., Grossman 1982; Rahel 1990; Fausch et al. 2002).

Alterations of assemblage structure viewed at small spatial and/or temporal scales may prove to be insignificant when viewed at larger more appropriate levels, and *vice versa*. Furthermore, long-term studies have rarely used continuous, structured sampling regimes throughout the focal study period. Rather, these studies have relied on isolated sampling periods, creating gaps within their temporal breadth. The need for continuous sampling to properly understand the interactions between environmental processes and stream fishes has been demonstrated by the riverscape principle (Fausch et al. 2002). Studies lacking these intermediate samples may be missing fluctuations and structural trends important in understanding how and why an assemblage has changed or remained temporally the same (e.g., Ross et al. 1985; Hansen & Ramm 1994; Berra & Petry 2006). Additionally, owing to the magnitude and complexity of many long-term data sets, studies are often limited to either temporal or spatial trends independent of one another. This is problematic because time and space are not independent with

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respect to variability in assemblage structure, and this is often overlooked in aquatic ecology (see Meador & Matthews 1992). As a result of the many confounding factors that may limit the understanding and quantification of ecological patterns, long-term structured surveys encompassing large areas are increasingly important for testing assemblage structure dynamics in aquatic systems.

Despite the substantial effort describing ecological assemblages across spatio-temporal scales, the processes responsible for structuring assemblages and the degree to which these processes contribute are still questioned. These processes are either stochastic or deterministic regulation of assemblage structure. Constancy within assemblage structure may be indicative of deterministic organisation, in which competitive exclusion among species is avoided through biotic processes such as resource partitioning or nonlinear competition within assemblages (Grossman 1982). Alternatively, stochastic structuring would yield unpredictable variability driven mainly by abiotic environmental processes, such that equilibrium would never be reached (Grossman et al. 1982). However, these processes may be system specific dependent on a stream's disturbance regime (Poff & Allan 1995).

Environmental instability is most commonly related to high levels of disturbance within a system. As generally defined by White & Pickett (1985), disturbances include any event that disrupts an ecosystem or assemblage structure and causes changes in natural resources or the physical environment. Gorman & Karr (1978) found that the assemblage structure in modified streams was very unstable as compared to that of undisturbed stream communities. Disturbance events such as altering watershed landscapes often influence changes in substrate type and stream sediment load (Karr et al. 1985; Sutherland et al. 2002), and impoundment and channelisation events influence assemblage structure through the alteration of natural flow regimes (Quinn & Kwak 2003; Gillette et al. 2005; Taylor et al. 2008). Hydrologic variability, specifically periods of extreme low flow, contribute to habitat loss as well as changes in water quality (Magoulick & Kobza 2003; Matthews & Marsh-Matthews 2003), which may alter assemblage structure.

River systems of the southeastern United States possess the greatest diversity of temperate freshwater fishes in the world (Warren et al. 1997). Many of these systems, however, have been subject to anthropogenic changes including the construction of impoundments, channelisation, in-stream sand and gravel mining (Phillips & Johnston 2004; Hayer & Irwin 2008; Taylor et al. 2008), as well as extreme natural environmental perturbations such as hurri-

canes, droughts and floods (Freeman et al. 1988; Mallin et al. 1999; Schaefer et al. 2006).

In this study, contemporary and historical fish collection data (1988–2009) from the Pearl River were used to assess the patterns of fish assemblage structure across both temporal and spatial scales. Data sets such as this, based on standard sampling protocol and periodicity maintained over the study period, are rare and provide an opportunity to examine how ecological systems are structured across generous scales. Here, we examined spatio-temporal patterns in assemblage structure and assessed the ways in which abiotic environmental events (i.e., drought and hurricane events) influence such patterns. Many studies have pointed out the importance of abiotic factors, including stream gradient and hydrologic variability, in structuring stream fish assemblages (e.g., Schlosser 1982; Poff & Allan 1995).

Our objectives were as follows: (i) To test for spatio-temporal differences in assemblage structure across the study period. (ii) To test whether spatially independent assemblages have complimentary structural dynamics across the temporal scale of study. We were interested in whether upstream and downstream assemblages covaried with respect to structural dynamics across time (i.e., whether assemblages shared patterns of structural change across time). (iii) To examine the effects of space on assemblage composition within the system. Here we tested similarity between upstream and downstream assemblages to characterise potential species differences between areas. (iv) To assess structural patterns across the temporal breadth of study and examine the contributions of environmental factors in structuring assemblages. As a result of the stochastic environmental events, including periods of low flow and the impacts of hurricanes on the system, it was predicted that there would be temporal alterations in assemblage structure associated with environmental perturbations. Furthermore, it was predicted that upstream and downstream assemblages would differ structurally owing to the influences of local features across the stream gradient.

Study area

The Pearl River is a Gulf coastal plain system located in Mississippi and Louisiana, USA (Fig. 1), drains approximately 22,688 km² and is nearly 640 km in length. It is a moderately diverse system that harbours approximately 119 different freshwater fishes, which is relatively high compared to other rivers of similar size in eastern Louisiana and southern Mississippi (Ross 2001). The ichthyofauna of the Pearl River system has been studied for more than half of a century (Gunning & Suttkus 1985, 1990, 1991; Love
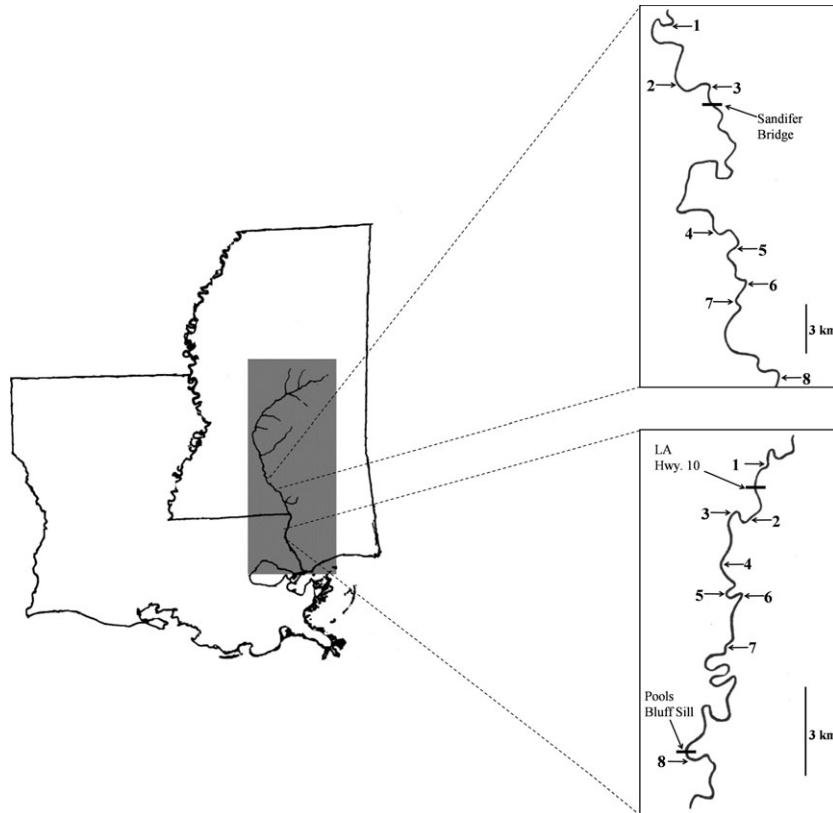
Fig. 1. Location of study sites in the Pearl River basin, Mississippi and Louisiana, USA. Boxes encompass the eight sites in the upper survey area and the eight sites in the lower survey area.

& Taylor 2004; Piller et al. 2004; Tipton et al. 2004; Stewart et al. 2005); however, no study has examined the assemblage structure dynamics of its fishes across time and space.

Since the 1950s, the Pearl River has been subject to many anthropogenic perturbations including mill effluent, dredging, snagging, navigation channel development, and dam and reservoir construction, which have threatened river channel stability and raised much concern for its fishes (Piller et al. 2004). The two most predominant modifications have been the construction of the Ross Barnett Dam in Jackson, MS (1960–1964) and the Pearl River navigation channel, completed in 1953 to be used as a shipping channel that paralleled the river. To maintain a navigable water level in the navigation channel at all times, a low head dam (Pools Bluff sill) was constructed across the river channel just downstream of the navigation channel connection site. The navigation channel is not presently in use or maintained. Furthermore, several natural environmental perturbations have occurred in the system including years of extreme drought in 2000 and 2007, and the impacts of Hurricanes Katrina and Rita in the summer of 2005. The impact of Hurricane Katrina was especially concerning because of its storm path which

notably travelled directly up the mouth of the Pearl River following the stream channel inland.

Materials and methods

Sample collections

This study incorporated both historic and contemporary fish collections from the main channel of the Pearl River. The historic data set was initiated in the 1950s by the late Dr Royal D. Suttkus (1920–2009), Emeritus Professor of Biology and Curator of Fishes, Tulane University. Sites were located on two stretches of the River, one near Monticello, Mississippi (Upper Pearl River survey) and the other near Bogalusa, Louisiana (Lower Pearl River survey) (Fig. 1). Sampling by Dr Suttkus ceased in August of 2005. However, sampling efforts were continued by personnel at Southeastern Louisiana University beginning in April 2006, through the end of 2009. Because of inconsistencies in sampling methods and localities used in early sampling periods, this study only incorporated data from 1988, when sampling methods were standardised to the current protocol. Sampling between 2006 and 2009 was carried out utilising this same standardised methodology.

Fish sampling was conducted quarterly at the same sixteen sites along the Pearl River between 1988 and 2009. Sites were divided among two separate areas of river, with each area containing eight sites (Fig. 1). During periods of low flow and other events rendering some sites inaccessible, comparable alternate sites were sampled in their place. The upper stretch was generally sampled during the months of February, May, August and November, and the lower stretch was generally sampled during the months of January, April, July and October. No collections were made in February 1989 or in any upstream sites in 1993 (February, May, August and November). Furthermore, no collections were made during the four sampling months following Hurricane Katrina (October 2005, November 2005, January 2006 and February 2006) or during January 2009.

Sample sites were located along the shoreline on the inner bends of the river, and each site was ~100 m in length. Fishes were collected from wadable habitat at each site using a 10-foot seine (10′ × 6′, 3/16″ ace mesh). Each site was sampled for approximately 15 min. All fishes collected were immediately fixed in 10% commercial grade formaldehyde. After fixation, collections were then transferred to water for sorting and identification. Specimens were identified to species level in all cases except for the genus *Carpiodes* which were pooled per collection site (i.e., these were usually collected as young of year and were not reliably identifiable to species). All specimens were then placed in 70% ethanol and permanently archived in the Royal D. Suttkus Fish Collection at the Tulane University Museum of Natural History (1988–2005) or the Southeastern Louisiana Vertebrate Collection (2006–2009).

Data analysis

Nonparametric statistical analyses, including nonmetric multidimensional scaling (nMDS) and hierarchical cluster analyses, were used to assess patterns in assemblage structure across the temporal and spatial scales of study. These methods were chosen because they are complementary to one another, each working off of the same resemblance matrix, which provided a more reliable assessment of assemblage structure than either analysis on its own. Additionally, analysis of similarity (ANOSIM), permutational multivariate analysis of variation (PERMANOVA), similarity profile (Simprof), similarity percentage analysis (SIMPER) and BEST analysis were used to quantify structural distinctions across scales of study. The use of nonparametric statistical analyses allowed comparisons to be made while avoiding the assumptions of normality and homogeneity, yielding a more realistic approach towards quantifying assemblage structure in a natural system. Statistical analyses were performed using PRIMER 6 (Plymouth Routines In Multivariate Ecological Research) (2008 PRIMER-E Ltd, Plymouth, UK). The PRIMER statistics package has been commonly used for aquatic community data analyses (see Clarke & Gorley 2006; Humphries et al. 2008; Huntington et al. 2010; Fodrie & Heck 2011; Perkin & Bonner 2011).

Spatio-temporal variation of assemblage structure

We performed a two-way crossed analysis of similarity (ANOSIM) to determine significant differences of years across areas, and areas across years. This was run using a maximum of 999 permutations per group (i.e., year) pair-wise comparisons. Sites were *a priori* classified as either upper (Monticello) or lower (Bogalusa) areas. Moreover, sites within each sampling period (i.e., eight sites per sampling period) were combined because of the absence of an area effect between sites within each sampling period (this was determined based on a nested ANOSIM previously run on the raw data). Global R values and associated *P* values were reported (Clarke 1993). R values range from −1 to 1, where −1 indicates all within-group similarity is less than among group similarity, and 1 indicates all within-group samples are more similar to one another than among group samples. This was based on mean rank similarity of groups. Groups were considered significant at *P* < 0.05. To assess the potential interaction between time and space, we ran a permutational multivariate analysis of variation (PERMANOVA) using 9999 randomisations. This analysis is similar to ANOSIM; however, it also provided an interaction term which allowed us to assess spatio-temporal relationships in assemblage structure (*see* Anderson 2001 for details). Prior to these analyses, all data were square root transformed, which decreased the overpowering effects of highly abundant species in the data set (see Appendix I for species composition), and a Bray–Curtis similarity resemblance matrix was created based on between sample comparisons. The Bray–Curtis coefficient is favoured in ecological community analyses because it obeys many rules of 'natural' biology and is not heavily influenced by shared zeros common in community data sets (*see* Clarke & Gorley 2006). This same approach was taken for all data sets herein (whether pooled over space/time or not).

To visualise the effects of area and time in a single analysis, we employed a method that allows the depiction of spatio-temporal relationships together. Samples from each study year were averaged, creating an individual sample for each year at each river area (e.g., lower 1988, upper 1988, etc.). This reduced random variation in the data set and aided in

reducing stress levels, rendering results more interpretable in subsequent nMDS analyses (High stress levels > 0.15 are indicative of poor depiction of data in two dimensional space). nMDS was run from the resemblance matrix using 50 restarts and a minimum stress value of 0.01. This enabled a clear representation of the upper river area in relation to the lower river area, as well as an across year representation in two dimensional space.

Spatial comparisons of assemblage structure

To determine whether spatially independent assemblages show complimentary structural dynamics across time, we employed the RELATE routine. Separate resemblance matrices were created for each of the upper and the lower areas. Matrices were compared to one another through RELATE analyses, which captures sequential structure (in this case years) in assemblage data that covary between sampling areas (i.e., the algorithm searches for similarity between resemblance matrices). RELATE analysis is a nonparametric version of a Mantel test. This analysis produces a Rho sample statistic which indicates the probability of the pattern occurring by chance alone. A ρ value approaching 1 indicates covariance in assemblage structure across years, between areas. ρ values were interpretable at $P < 0.05$.

To characterise the effects of space on assemblage composition within the system, we ran similarity percentage (SIMPER) analysis (Clarke 1993). This was run comparatively between upper and lower area assemblages using the previous similarity matrix (i.e., sites within sampling periods combined). Average dissimilarity percentages between groups, and average dissimilarity percentages of the contributing species were reported. SIMPER provides average abundances of species within each area and the standard deviation divided by the average dissimilarity of each species. Therefore, a species with a high average dissimilarity and a low standard deviation is a good contributor to the differences between areas. Species contributing to the majority of dissimilarity (>90%) were reported.

Temporal patterns of assemblage structure

Because spatial differentiation between areas may be disruptive in illustrating assemblage structure across time alone, the following analyses were conducted in the absence of area differences. This was deemed appropriate based on previous findings in RELATE analysis (depicted in results).

Rarefied species richness and total per year abundance were each graphed as regression models across sample years. Estimates of rarefied species richness were based on 7000 individuals for each collection year (7000 was used because at least this many individuals were collected each year). Individual samples for each year of study (1988–2009) were created by averaging site collections per year. nMDS was run, in addition to hierarchical complete linkage cluster analysis coupled with a similarity profile (Simprof) test of significance. Simprof tested for genuine internal structure within the resultant dendrogram. Simprof creates a similarity profile by ranking the similarity matrix. A mean profile is then calculated by randomising (1000 permutations) the order of each variable value and recalculating the profile. The mean profile is compared against the actual similarity profile yielding the summed absolute distances (π) between the two dendrograms. This was compared with the deviations of further randomly generated profiles (=999) to test for significance. Group significance was tested at $P < 0.05$. Simprof is *a priori* unstructured and therefore allows comparisons between individual samples rather than between predefined groups (see Clarke et al. 2008 for further description). Additionally, a cophenetic correlation was run to determine the cluster quality.

The BEST routine was run to find species most influential on assemblage structure across time. The procedure measures the agreement between the overall Bray–Curtis dissimilarity measures for the entire community and those of the individual species. This is performed using spearman rank correlation method which uses stepwise comparisons to measure similarity between the two matrices. The results give a list of the most explanatory variables, in this case species. Mean per site abundances (square root transformed) were plotted across years for influential species.

Hydrology

We quantified stream hydrology using United States Geological Survey (USGS) discharge ($m^3 \cdot s^{-1}$) data obtained from two gauging stations on the Pearl River, one located in Monticello, MS (Upper Pearl River survey area USGS 02488500) and the other in Bogalusa, LA (Lower Pearl River survey area USGS 02489500). Annual mean discharge was graphed for each area across the study period. To assess possible effects of hydrologic variation on assemblage structure, we examined the relationship between annual discharge and nMDS axis scores from prior analysis, using spearman correlation methods. Because the timing of extreme flow events can determine how and to what degree a community is impacted (Durham & Wilde 2009; Taylor 2010), we also examined differences in seasonal discharge across years using mean daily discharge ($m^3 \cdot s^{-1}$) data.

Mean daily discharge was $\log_{10}$ transformed to standardise across years. The addition of these data allowed correlations between assemblage structure dynamics and discharge variability during years of extreme low discharge.

Results

A total of 698,609 fish specimens were collected from the Pearl River between January 1988 and November 2009, including 98 species (Appendix I). Over the 22-year sampling period, 6 species accounted for 90.54% of the specimens collected. These included *Cyprinella venusta* (54.57%), *Hybognathus nuchalis* (10.14%), *Pimephales vigilax* (9.28%), *Notropis volucellus* (6.39%), *Notropis longirostris* (5.72%) and *Notropis texanus* (4.44%). All other species collected made up <10% of the total collections.

Overall abundance of specimens collected decreased across the sample period, with an initial abundance total of 50,362 in 1988, and a final yearly abundance of 9543 in 2009 ($r^2 = 0.45$) (Fig. 2a). The highest abundance occurred in 1995 (56,091) and the lowest in 2006 (7,819). There was also an overall decrease in rarefied species richness across all years ($r^2 = 0.39$) (Fig. 2b).

Spatio-temporal variation of assemblage structure

The two-way ANOSIM that tested data in a crossed layout, with locations and years as factors, reported significant year groups across areas (global $R = 0.192$, $P < 0.001$) and significant area groups
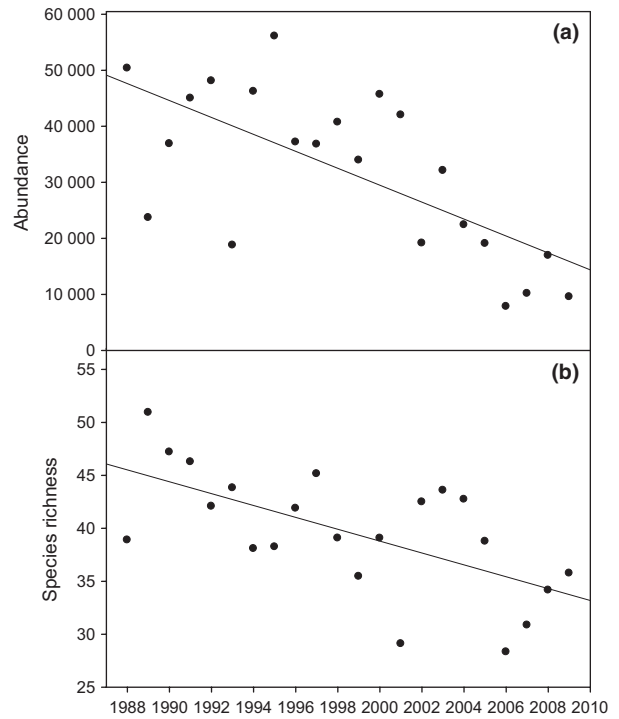

Fig. 2. (a) Annual cumulative abundances of specimens collected in the Pearl River across the temporal sampling period (1988–2009) ($r^2 = 0.45$, $F(1,20) = 16.67$, $P < 0.001$). (b) Annual rarefied species richness of fishes in the Pearl River across the sampling period (1988–2009) ($r^2 = 0.39$, $F(1,20) = 13.03$, $P = 0.0017$). Solid lines are least-square regressions.

across years (global $R = 0.231$, $P < 0.001$). The similar global R values for years and areas indicate that both factors have similar magnitudes of contribution to assemblage structure differences. The PERMANOVA
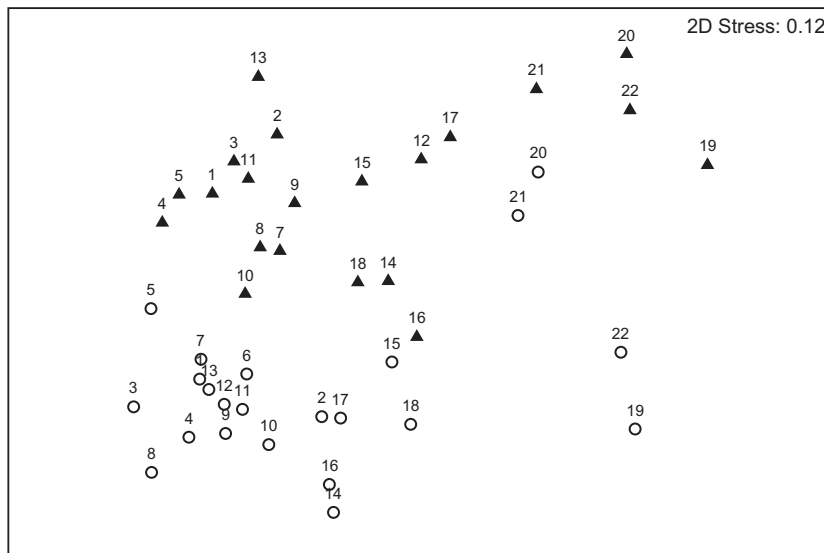

Fig. 3. nMDS depicting the relationship between the upper and lower survey areas of the Pearl River from 1988 to 2009. Triangles correspond to the upper survey area, and circles correspond to the lower survey area. Numbers 1–22 correspond to sample year (1 = 1988, 2 = 1989, 3 = 1990, *etc.*).

reported a nonsignificant time*area interaction ($P = 0.99$). Nonmetric multidimensional scaling (nMDS) further depicts the relationship of time and space across the system (Fig. 3).

Spatial comparisons of assemblage structure

RELATE analysis found significant correlation between assemblage structure dynamics of the two areas based on sequential resemblance matrix similarities across years. The analysis reported a sample statistic (ρ) of 0.681 at a significance level $P < 0.001$.

Similarity percentage (SIMPER) analysis determined average within-group similarities of 59.29% and 58.17% for the lower and upper areas, respectively. The average dissimilarity between the upper and lower areas was 45.27%. Species yielding the greatest average dissimilarities between upper and lower areas included several minnow species (Cyprinidae), as well as the sand darter *Ammocrypta beanii*, and the sunfish *Lepomis megalotis* (Table 1).

Temporal patterns of assemblage structure

Multidimensional scaling (nMDS) showed inconsistency of assemblage structure across sample years (Fig. 4). This is further recognised by the cluster analysis (cophenetic correlation coefficient = 89.2%), which revealed three distinct groupings based on the Simprof test. Significant year groups included: (2006–2009) which was distinct from all other year groups at $P < 0.001$; and (2001–2005) which was distinct from 1988 to 2000 at $P = 0.012$. All significant groups contained at least 66.89% within-group similarity, and the overall similarity among all groups was 52.86%. BEST analysis reported five species most responsible for the data structure depicted in the nMDS analysis. These species included: *Cyprinella venusta, Hybognathus nuchalis, Notropis texanus, Pimephales vigilax*, and *Macrhybopsis aestivalis*. Species generally indicate greater abundances in earlier years and lower abundances, or loss of abundance in the more recent study years (Fig. 5).

Table 1. Results from SIMPER analysis showing the species contributing most to the differentiation between the upper and lower areas (total average dissimilarity between upper and lower = 45.27%).

| Species	Lower area average abundance	Upper area average abundance	Average dissimilarity	Dissimilarity/ SD	Contribution %	Cummulative %
Cyprinella venusta	15.95	15.49	6.36	1.35	14.04	14.04
Hybognathus nuchalis	7.00	3.17	4.78	1.07	10.57	24.61
Pimephales vigilax	6.40	5.10	3.47	1.22	7.67	32.28
Notropis volucellus	4.79	4.10	3.31	1.19	7.32	39.59
Notropis texanus	4.96	1.50	3.29	1.15	7.27	46.87
Notropis longirostris	4.66	5.10	2.30	1.15	5.08	51.95
Notropis atherinoides	3.36	1.44	2.12	1.14	4.68	56.63
Ammocrypta beanii	3.40	1.78	1.66	1.28	3.67	60.30
Lepomis megalotis	1.44	2.60	1.35	1.12	2.99	63.29
Gambusia affinis	1.63	1.52	1.29	0.95	2.86	66.15
Macrhybopsis storeriana	1.28	0.27	0.95	1.11	2.09	68.24
Carpiodes sp.	0.92	1.16	0.88	1.17	1.94	70.18
Micropterus punctulatus	0.69	1.36	0.80	1.20	1.77	71.95
Trinectes maculatus	0.87	0.00	0.72	1.17	1.58	73.53
Macrhybopsis aestivalis	0.74	0.27	0.70	0.49	1.54	75.07
Hybopsis winchelli	0.70	0.73	0.67	1.10	1.48	76.55
Labidesthes sicculus	0.62	0.72	0.59	1.11	1.31	77.86
Dorosoma petenense	0.39	0.52	0.59	0.60	1.31	79.16
Percina sciera	0.85	0.74	0.58	1.23	1.29	80.45
Ictalurus punctatus	0.47	0.57	0.55	0.93	1.22	81.67
Percina vigil	0.70	0.40	0.54	1.15	1.18	82.85
Opsopoeodus emiliae	0.66	0.23	0.53	0.94	1.17	84.03
Lepomis macrochirus	0.51	0.70	0.52	1.08	1.16	85.18
Fundulus notatus	0.20	0.58	0.51	0.84	1.12	86.30
Micropterus salmoides	0.32	0.39	0.40	0.73	0.88	87.18
Etheostoma swainii	0.44	0.07	0.35	0.98	0.77	87.95
Dorosoma cepedianum	0.12	0.33	0.32	0.50	0.70	88.65
Ammocrypta vivax	0.35	0.13	0.29	0.98	0.64	89.29
Fundulus catenatus	0.00	0.30	0.26	0.79	0.58	89.86
Pomoxis annularis	0.12	0.24	0.24	0.67	0.52	90.39
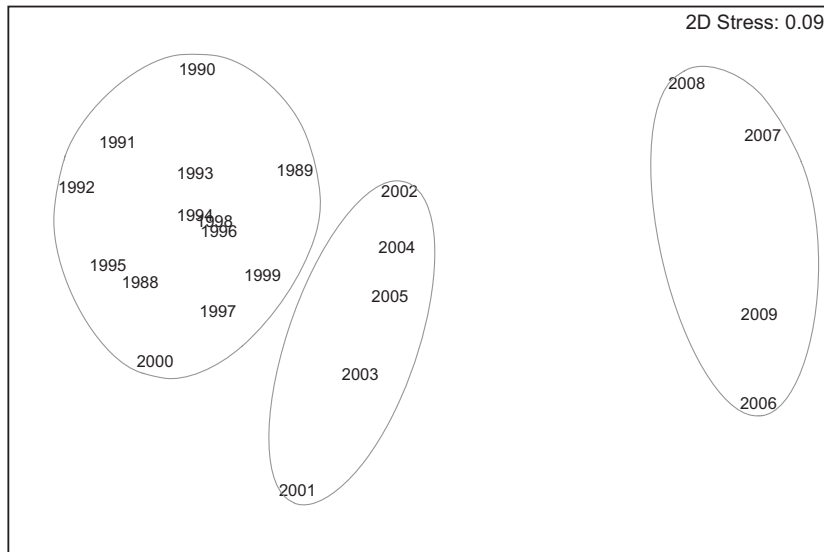
Fig. 4. nMDS of fish assemblage structure (upper and lower survey areas combined) across the study period (1988–2009). Groups found to be significant based on the Simprof test from cluster analysis are encircled.
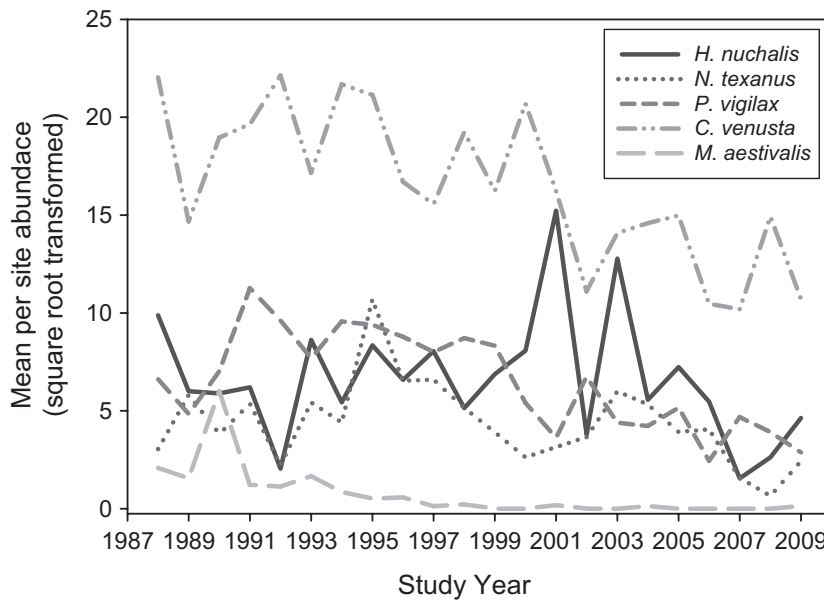

Fig. 5. Abundances of species found to be most influential on assemblage structure across years (based on BEST analysis results). Plots represent average species abundance for each site (square root transformed) within each year of the study.

Hybognathus nuchalis, however, was an exception yielding its greatest abundance in 2001 (Fig. 5).

Hydrology

Mean annual discharge data indicated 2 years of extreme low discharge, 2000 and 2007. The lowest discharge year was 2000, with a recorded average discharge of 101.00 $m^3 \cdot s^{-1}$ in the lower area and 65.69 $m^3 \cdot s^{-1}$ in the upper area. In 2007, mean annual discharge was also considerably lower than that of other study years, with an average discharge of 131.50 $m^3 \cdot s^{-1}$ in the lower area and 71.95 $m^3 \cdot s^{-1}$ in the upper area (Appendix II). When compared against the axes scores of the prior nMDS (Fig. 4), we recovered no significant correlations between assemblage structure and discharge. We did however find that the shift we observed in assemblage structure in 2001 follows the lowest discharge year of the study (Fig. 6). When we compared mean daily discharge of the entire study period to that of the two drought years (2000 and 2007), we found differentiations between seasonal flow patterns (Fig. 7). Daily discharge in 2000 did not show the peak spring flow pattern observed in other years. Instead, discharge was uncharacteristically low during the beginning of
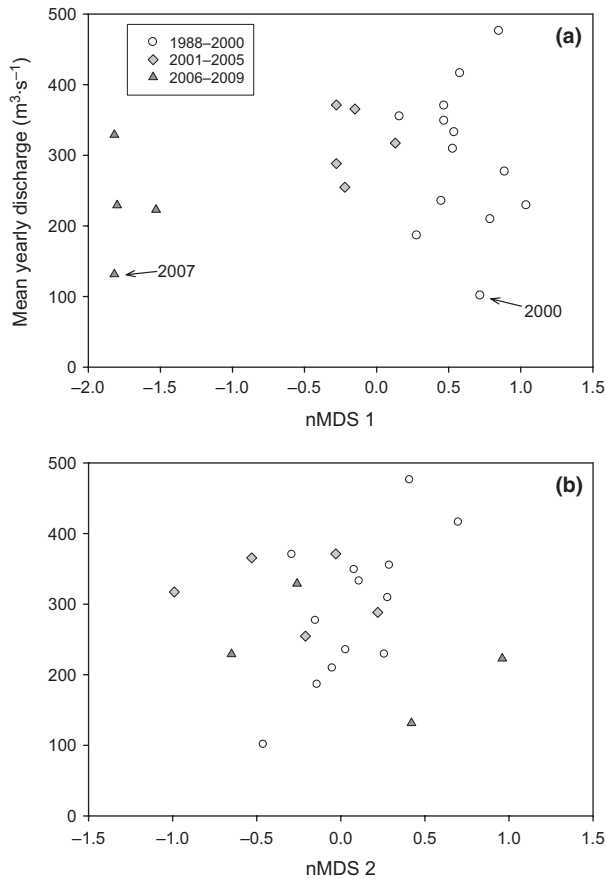
Fig. 6. Plots of the relationship between mean annual discharge $(m^3 \cdot s^{-1})$ and nMDS axes scores describing assemblage structure. (a) nMDS axis 1 scores versus mean annual discharge. (b) nMDS axis 2 scores versus mean annual discharge.

Fig. 7. The Log_{10} mean daily discharge $(m^3 \cdot s^{-1})$ across all study years in each the upper and lower areas. Mean daily discharge is represented by black hashes, and the surrounding grey area is the standard deviation of daily means across years. Additionally, daily means for drought years (2000 and 2007) were overlaid for both the upper and lower areas.

2000. Discharge in 2007, however, did not share this uncharacteristic trend, but instead followed a similar trend as seen in other years (Fig. 7).

Discussion

In this study, results indicated a differing species composition between the upper and lower areas; however the changes in assemblage structure across time occurred in a similar manner (Fig. 3). Although time was assessed independently later in the study, such analyses may have been deemed inappropriate without the knowledge of the spatio-temporal interaction at hand (i.e., because no time × space interaction was recovered, and both the upper and lower areas significantly shared the same temporal pattern, combining years was acceptable and aided in describing temporal relationships).

The similar structural trends found between the upper and lower areas across the study period indicated that assemblages of each area have experienced shifts in structure at similar temporal intervals despite the observed differences in assemblage composition betwe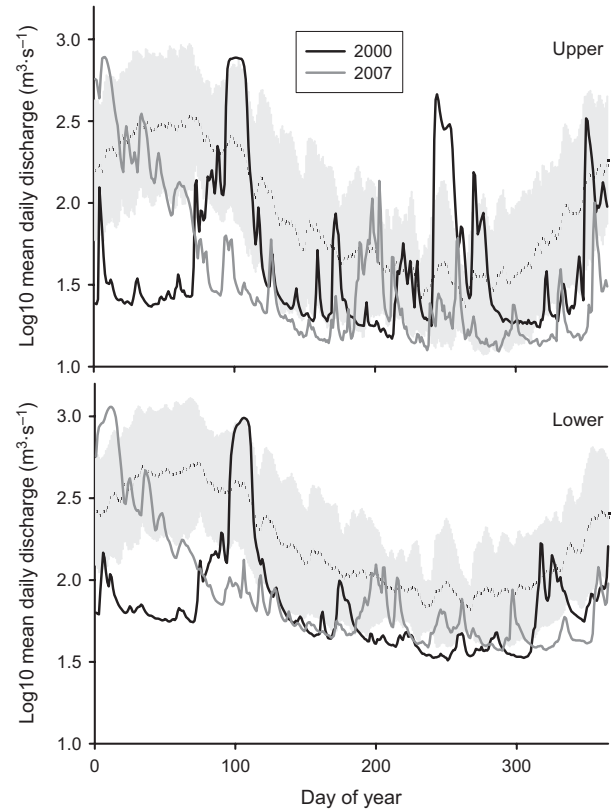en the upper and lower areas. Moreover, both areas showed similar lack of assemblage equilibrium across time, as depicted by nMDS (Fig. 4) (i.e., early years differed structurally from more recent years). In general, a spatial distinction, as well as within-area temporal distinctions, was observed (as demonstrated by ANOSIM). Hansen & Ramm (1994) recovered similar results yielding a distinction between upstream and downstream areas, as well as similar within-area temporal distinctions in a New York stream; however, their study lacked continuous sampling effort across its temporal scope.

The significant spatial differentiation observed between the two study areas indicates strong geographic influences on local fish assemblages. This differentiation may be influenced by differing geomorphologies of the river channel following the spatial gradient of study. For example, Gorman & Karr (1978), and Schlosser (1982) found an increase in assemblage and habitat diversity following the stream-order gradients in multiple streams. Factors including differing flows and stream area may also lead to variability in habitat choice and availability between areas as indicated by Magoulick & Kobza (2003). In our study, species that contributed most to

area differences include greater abundances of multiple pelagic minnows (Cyprinidae) and one species of darter (Percidae) *Ammocrypta beanii* in the lower area, and greater abundances of *Lepomis megalotis* (Centrarchidae) in the upper area. Species characterising the lower area tend to prefer structurally simple habitats (i.e., habitats lacking in stream debris and vegetation), whereas species characterising the upper area may be more preferential towards habitats with the addition of vegetation and woody debris (Ross 2001). This corroborates the river continuum concept, where as stream discharge increases, the proportion of woody debris and vegetation to discharge decreases (Vannote et al. 1980). However, this is only speculative owing to the lack of habitat variables collected across the study period.

When viewed across the temporal scale of study, the Pearl River fish assemblage was characterised by a general decrease in both species richness and abundance between 1988 and 2009. Our analyses yielded two large deviations in assemblage structure which were depicted as sequential group 'breakups' across years. These two significant alterations in assemblage structure were correlated with environmental perturbation events. The first event being a drought year in 2000, which was followed by alterations of abundances of several species as well as a decrease in species richness in 2001 (Fig. 2b). Although our results depict two drought years (2000 and 2007) across the frame of study, we only found a disruption in seasonal discharge pattern in 2000. Years characterised by low flow have been shown to strongly affect recruitment and young of year survival in many stream fishes (Freeman et al. 1988; Matthews & Marsh-Matthews 2003). However, the timing of annual discharge regime also plays a key role in determining biological impacts (Durham & Wilde 2009; Taylor 2010). A large portion of temperate stream fishes spawn during peak spring flows (Ross & Baker 1983; Zeug & Winemiller 2008), and years lacking these spring flows may cause alterations in community structure. Our data suggest that the low discharge and uncharacteristic flow pattern observed in 2000 altered recruitment in many species, causing decreases in abundances of many species the following years (this is further discussed later).

The second alteration in assemblage structure occurred following the impacts of Hurricanes Katrina and Rita in August and September of 2005. Our results report a divergence in fish assemblage structure following the hurricanes of 2005, which is further characterised by a sharp decrease in species richness in the following year (Fig. 2b). Although the effects of hurricanes on fishes of freshwater systems have not received much focus, existing studies indicate a need for attention. Schaefer et al. (2006) found fish assemblage structural changes in the neighbouring Pascagoula River, a basin with a nearly identical ichthyofauna to the Pearl, following Hurricane Katrina. Mallin et al. (1999) reported the effects of multiple hurricanes in the Cape Fear watershed, NC, including decreased dissolved oxygen levels and massive fish kills. During hurricane events, biological oxygen demand increases because of high woody and leaf debris input. Moreover, heavy flooding may cause increased erosion and thereby sedimentation and nutrient loading in streams (Mallin et al. 2002). The Pearl River experienced a dramatic spike in discharge as hurricane Katrina moved inland in late August of 2005 (Appendix III). This was a rather dramatic hydrologic fluctuation considering it occurred during the summer when discharge is normally minimal. Such a sudden increase in discharge was likely accompanied by increased in-stream debris and sediment loading. Following the impact, fish kills were reported in the system (Mississippi DEQ 2006), which likely contributed to the alterations in assemblage structure seen thereafter.

Species found to be most influential on assemblage changes across time generally showed the pattern of decreasing abundances. However, some species show stable abundances within year clusters including *Cyprinella venusta* and *Pimephales vigilax*. This indicates a more direct effect of environmental disturbances (drought and hurricane) rather than a gradual loss of abundances. Both *C. venusta* and *P. vigilax* are non-benthic substrate generalists (Ross 2001) and are therefore not as reliant on specific substrata for most ecological functioning. However, both *C. venusta*, crevice spawning (Pflieger 1975), and *P. vigilax*, egg-clustering (Page & Ceas 1989), do rely on substrate availability for reproduction. During low flow periods, as seen in 2000, there may have been less available substrate for reproductive efforts of these species, contributing to the declines in abundances in following years. *Macrhybopsis aestivalis*, a benthic sand-gravel specialist, was relatively abundant during early years of the study, but was rarely collected following 1996. This loss in abundance was not correlated with any specific environmental event and instead was gradual. Piller et al. (2004) reported *M. aestivalis* as being extremely abundant in the Pearl River prior to 1988, when it was the third most abundant species collected during earlier surveys (1955–1988). Previous studies (Berkman & Rabeni 1987; Tipton et al. 2004; Stewart et al. 2005) found similar decreases and/or losses of benthic species, acknowledging instability within the stream channel as a possible contributor. Many stream modifications including dredging, snagging, navigation channel development and dam and reservoir construction have occurred in the Pearl River, which may be responsible for geomorphic instability.

Despite the decreases in the abundance of many species following the drought of 2000, *Hybognathus nuchalis* showed a sharp increase in abundance. The observed increase in *H. nuchalis* may be partially explained by its diet, which was described as bottom ooze by Whitaker (1977), and includes sand, silt, fungal material, decaying plant material and diatoms. In a degraded system following drought conditions, species such as *P. vigilax, N. texanus* and *C. venusta*, whose diets consist partially of insects and or insect larvae (Hambrick & Hibbs 1977; Whitaker 1977; Felley & Felley 1987; Ross 2001), may have struggled to find food resources. As noted by Matthews & Marsh-Matthews (2003), the effects of drought on fishes may be partially driven by changes in invertebrate food availability. This is based on the suggestion that many aquatic invertebrates are also negatively affected by drought conditions, including declines in abundance (Griswold et al. 1982). The less limiting, readily available diet of *H. nuchalis* may have allowed increased survival during periods of drought resulting in higher abundances within the following year. Not much is known of *H. nuchalis* reproductive biology; however, the increase in abundance could be linked to some beneficial reproductive timing and/or spawning strategy. Lehtinen & Leyzer (1988) found spawning to be stimulated by abrupt rises in flow in populations of *Hybognathus placitus* in the Midwestern United States. A study by Turner et al. (2010) found poor recruitment of *Hybognathus amarus* in the Rio Grande during a year when no spring flood pulse occurred. The following year under spring flood conditions, *H. amarus* comprised a dominant portion of the spring larval assemblage. It is possible that the closely related *H. nuchalis* may have spawned at a more beneficial time of greater flow during the drought period, diminishing the chance of egg mortality through desiccation, and increasing survivorship into the next year. Moreover, *H. nuchalis* produce nonadhesive pelagic embryos that freely flow with current (Simon 1999). This may further aid in embryo survival during receding water levels, as they are able to move with the water level, rather than being 'left out to dry'.

Previous studies have reported alteration of assemblage structure as a consequence of environmental disturbances (e.g., Ross et al. 1985; Matthews 1986). Furthermore, many of these studies noted recovery following disturbance events (Ross et al. 1985; Matthews 1986). Our study suggests a lack of recovery in assemblage structure across time. Although assemblage structure did not recover within the system, we did see recovery in species richness and overall abundance shortly following environmental perturbation events. The alterations in assemblage structure following environmental fluctuations would seem to support the idea of a stochastic structuring process within assemblages across time (Grossman et al. 1982), rather than deterministic organisation (Grossman 1982). However, we did find that assemblage structure maintains some within-group organisation for substantial periods prior to and following environmental events. This indicates that between perturbations other processes (i.e., biotic interactions) may play a role in assemblage organisation in the absence of extreme environmental fluctuations. Strange et al. (1992) found a similar alternation between stochastic and deterministic processes in a California fish assemblage, rather than a single persistent equilibrium.

In conclusion, this study revealed assemblage structural distinctions across both the temporal and spatial breadth of investigation. The assessment of distinct spatio-temporal patterns in the fish assemblage of the Pearl River over nearly a quarter of a century is indicative of significant change in comparison with normal variability. The recovered shifts in assemblage structure across time further support the idea that environmental perturbation events, both historical (i.e., dam construction and channel modifications) and contemporary (i.e., droughts, floods and hurricanes), do play vital roles in structuring assemblages. This study illuminates the importance of large temporal and spatial scales when assessing patterns of assemblage structure. The structural differentiations we recovered may have easily gone undetected at lesser scales. Furthermore, the continuous standardised sampling regime used across the entire breadth of study allowed an intimate characterisation and complete historical account of assemblage structure rarely seen in other long-term studies.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix SI. Species composition, including total abundance and abundance percentage for each species collected across the study period.

Appendix SII. Mean annual discharge ($m^3 \cdot s^{-1}$) of the Pearl River 1988–2009, based on USGS gauge data.

Appendix SIII. The Log_{10} mean daily discharge ($m^3 \cdot s^{-1}$) across all study years in each the upper and lower areas.

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