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ARTICLE

Diel Turnover of Assemblages of Fish and Shrimp on Sandbanks in a Temperate Floodplain River

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Abstract
Seven sandbanks in the main channel of the Brazos River, Texas, were sampled a total of 35 times during both day (1800–1900 hours) and night (2200–2300 hours) in June and July 2008 to examine the diel turnover of fish assemblages. Day samples had an average of 10.1 species, whereas night samples had an average of 12.9 species. Average abundance (catch per unit effort, here defined as the number of individuals per 10-m seine haul) for day samples was 41.5, compared with 80.5 for night samples. Species richness and abundance were significantly greater on sandbanks at night. Additionally, nonmetric multidimensional scaling analysis and cluster analysis indicated consistent differences in assemblage structure between day and night samples. Most of the diel change in assemblage structure was due to ictalurids and palaemonids (freshwater decapod crustaceans) that were only common on sandbanks nocturnally. Catastomids, clupeids, cyprinids, and poeciliids were present on sandbanks both diurnally and nocturnally. Species that exclusively use sandbank habitats may be foraging during the day and seeking refuge from predators at night. Nocturnal species apparently move onto sandbank habitats at night for foraging and then migrate to deeper, more structurally complex habitats during the day to escape predation. Diel turnover of sandbank fish assemblages may be a general phenomenon in lotic ecosystems, but it is apparently not as pronounced in temperate rivers as in tropical rivers. Diel changes in habitat use deserve greater study because species assemblage structure and habitat use are the basis for ecological niche models used to predict species distributions based on climate change scenarios as well as physical habitat simulation models designed to determine instream flows.

Diel turnover of fish species assemblages has been observed in temperate coastal waters (Robertson 1980; Burrows et al. 1994), estuaries (Nash 1986), lakes (Helfman 1981), and streams (Salas and Snyder 2010), as well as subtropical and tropical coral reefs (Hobson 1973; Helfman 1978; Rooker et al. 1997), mangroves (Rooker and Dennis 1991; Lin and Shao 1999), and floodplain rivers (Arrington and Winemiller 2003). Shifts in light intensity at dawn or dusk or in association with lunar phases frequently influence the behavior of fish. Fishes that have well-developed visual systems often are inactive at night, and those that have well-developed olfactory and tactile systems often are inactive during the daytime. However, some species can alter their diel behavior to maximize growth and survival independent of their morphological adaptations. For example, contrasting diel activity patterns have been found to occur in the same species in different populations (Valdimarsson et al. 2000) and in different life history stages within the same population (Gries et al. 1997).

Three hypotheses are commonly invoked to explain the adaptive significance of diel changes in community structure within habitats: avoidance of competitors, avoidance of predators, and changes in resource availability. Competitive-induced changes in diel activity patterns implies that diel turnover is a type of resource partitioning, with species using the same resources but at different times of day (Kronfeld-Schor et al. 2001). Predator-induced diel shifts in habitat use can result from a trade-off between predation risk and optimal foraging (Lima and Bednekoff 1999; Clark et al. 2003). Prey can thus optimize their fitness by

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allocating their time between habitats with little risk of predation when predators are active and habitats with good foraging opportunities when predators are inactive (Hugie and Dill 1994). Finally, diel shifts in the quantity of resources may induce a subsequent shift in the period of time when their consumers are most active in order to maximize foraging efficiency (Metcalfe et al. 1999). For example, in northern Sweden, the diel activity patterns of the common merganser *Mergus merganser* and three species of gulls—the common or mew gull *Larus canus*, the herring gull *L. argentatus*, and the lesser black-backed gull *L. fuscus*—are closely associated with nocturnal spawning of their river lamprey *Lampetra fluviatilis* prey (Sjöberg 1989).

Studies of diel variation in fish assemblage structure in floodplain rivers have frequently documented two behavioral groups that seem to be associated with a tradeoff between predator avoidance and resource availability: fishes that use shallow littoral habitats exclusively and fishes that only use shallow littoral habitats nocturnally (Sanders 1992; Copp and Jurajda 1993; Kubecka and Duncan 1998; Arrington and Winemiller 2003; Wolter and Freyhof 2004). Besides being of theoretical interest, quantification of how fishes use different habitats in floodplain rivers is essential for management. Fish assemblage structure and habitat use are the foundation for ecological niche models used to infer the effects of climate change and for physical habitat simulation models used as a basis for instream flow management (Spence and Hickley 2000). In the present study, seven sandbanks in the main channel of the Brazos River, Texas, were sampled a total of 35 times during both day and night to quantify diel variation in species richness, abundance catch per unit effort (CPUE), and assemblage structure. Given the relative uniformity of sandbank habitats, we predicted that fish assemblage structure would be influenced more strongly by diel sampling period than by sampling locality.

STUDY AREA

The Brazos River flows from Blackwater Draw, New Mexico, to the Gulf of Mexico and is the 11th longest river in the United States, with a basin area of 116,000 km^2 and an estimated length of 2,060 km. In the river's middle and lower reaches, the hydrologic regime is essentially unpredictable; however, long-term median flows indicate that winter and spring tend to have higher flows than other times of the year (Zeug and Winemiller 2008). The physicochemical characteristics for the Brazos River include high nutrient concentrations, moderate pH, and fine sediment grain size that limits primary productivity during periods with high flows and turbidity. An estimated 45 fish species commonly occur in the main channel and floodplain lakes in the middle reach (Winemiller et al. 2000; Zeug et al. 2005).

METHODS

Sample collection.—Fish samples were collected from sandbanks in the Brazos River in June and July 2008 (Figure 1). During the study period, discharge ranged from 13.6 to 84.1 m^3/s. Sandbanks are point bars that form on the low velocity side of meanders and in our study reach ranged in length from approximately 300 to 900 m. Sandbanks were sampled using a 10 × 2-m bag seine with 6.4-mm mesh in the wings and 3.2-mm mesh in the bag. Each sample was a composite of successive contiguous (nonoverlapping) seine hauls taken parallel to shore until no new species were collected (3–6 hauls). The total distance hauled for each location was estimated in meters. Day samples (taken on 3, 5, 10, 12, 25, and 26 June and 7 July) were collected between 1800 and 1900 hours, and night samples (taken on 3, 5, 9, 17, 19, and 26 June and 3 and 10 July) were collected between 2200 and 2300 hours. Three sets of samples were collected on sandbanks during the day and then collected on the same set of sandbanks again after nightfall. Overall, 17 day samples and 18 night samples were obtained.

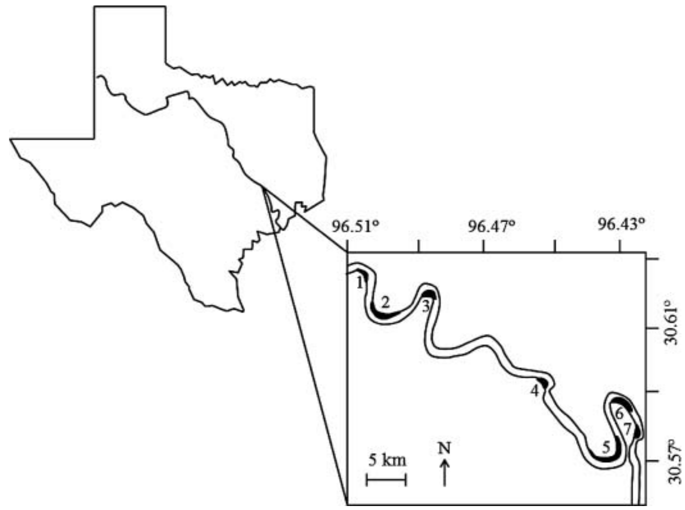

FIGURE 1. Location of the study site on the Brazos River. Shaded areas 1–7 denote the sandbanks where fish and shrimp assemblages were sampled both during the day and at night in June and July 2008.

For each sample, fish specimens were measured and placed into body size categories based on standard length (large, >11 cm; medium, 4–11 cm; small <4 cm). Large fish were identified in the field and released. Small and medium fish were euthanized by emersion in a 1% solution of tricaine methanesulfonate (MS-222), preserved in 10% formalin, and later transferred to 70% ethanol. Preserved specimens were identified and sorted in the laboratory. Some small juveniles could only be identified to genus (i.e., *Dorosoma*, *Ictalurus*, and *Lepomis* spp.). Specimens were archived in the Texas Cooperative Wildlife Collection at College Station.

Data analysis. —Species richness for each sample was estimated as the total number of species based on all seine hauls. Species abundances and the total distance seined per survey were used to estimate abundance CPUE, determined as the number of each species per 10 m of seine haul. The raw data were $\log_{10}(n + 1)$ transformed to meet the assumptions of normality before all analyses. A one-way randomized block analysis of variance

(ANOVA) was used to test for differences in species richness and abundance CPUE between diurnal and nocturnal samples and among different sandbanks (treatment = species richness or abundance CPUE, block = time of day and sandbank location).

Nonmetric multidimensional scaling (NMDS) analysis was used to explore the relationship between species assemblages based on abundance CPUE and diurnal and nocturnal periods. This type of analysis is a numerical technique that iteratively seeks a solution and then stops when the best fit ordination has been found (Holland 2008). Analysis of similarity (ANOSIM) was used to test for differences in assemblage structure between diel sampling periods and among the sampled sandbanks. Additionally, cluster analysis was used to evaluate whether diurnal and nocturnal abundance CPUE samples clustered separately. A Bray–Curtis dissimilarity matrix was used with the unweighted pair-group method with arithmetic mean (UPGMA) clustering method that uses average-linkage clustering. This method is less prone to chaining or to making compact clusters, and therefore is considered more objective in its groupings (Oksanen 2009). The NMDS analysis, ANOSIM, and UPGMA cluster analysis were performed with the software program R (R Development Core Team 2008). For all statistical tests, results were considered statistically significant if $P \leq 0.05$.

RESULTS

A total of 7,817 specimens were collected, representing 28 fish species and one decapod crustacean, the Ohio River shrimp *Macrobrachium ohione* (family Palaemonidae). All of the fish and the decapod crustacean species collected are native to Texas (Howells 2001). Smooth softshell turtles *Trionyx muticus* and Mississippi map turtles *Graptemys kohni* also were captured in the seine and subsequently released in the field. Because we wanted to focus on fish taxa for this study and because the turtle taxa (total number of individuals = 3) were rare compared with the decapod crustacean taxon (total number of individuals = 67), we did not include the turtle taxa in our final data set. The most abundant family collected both day and night was Cyprinidae, comprising 49.6% of the total abundance (Table 1). Species from the families Clupeidae and Cyprinidae were present in every sample collected. Species from the families Atherinidae, Lepisosteidae, Percidae, and Poeciliidae were more common in diurnal samples, and species from the families Ictaluridae, Palaemonidae, and Sciaenidae were more common in nocturnal samples.

Species Richness and Abundance

Nocturnal samples were significantly richer in species than diurnal samples (ANOVA: $F_{35,1} = 11.877$, $P < 0.01$). Whereas day samples had an average of 10.1 species, night samples had an average of 12.9 species. For both day and night samples, species richness estimates did not differ significantly among the seven sandbank locations (ANOVA: $F_{35,6} = 1.203$, $P = 0.34$).

Out of the seven groups of fishes that contributed most to the diel differences in mean abundance CPUE (listed in order of decreasing difference), small *Dorosoma* spp. and red shiners were more common in day samples than in night samples, and small *Ictalurus* spp., channel catfish, shoal chubs, Ohio River shrimp, and blue catfish were more common in night samples (Figure 2). Small catfishes were particularly common in some night samples; for example, a single night sample had 303 individuals. In comparison, the greatest number of small catfishes captured during diurnal sampling was 14 individuals. Ohio River shrimp also were active on sandbanks at night, with all specimens captured during night sampling.

Abundance CPUE (number of individuals/10-m seine haul) was significantly greater in night samples than day samples (ANOVA: $F_{35,1} = 8.806$, $P < 0.01$). Average abundance CPUE of day samples was 41.5 (SD = 25.0), compared with an average abundance CPUE of 80.5 (SD = 68.8) for night samples. This was mostly due to the high nocturnal abundance of a few species. For example, in only one instance did a day sample have a taxon CPUE greater than 50 (bullhead minnow), whereas nocturnal abundance CPUE exceeded 50 for small catfishes in five samples and red shiners in one sample. Abundance CPUE did not differ significantly among the sandbanks (ANOVA: $F_{35,6} = 0.779$, $P = 0.59$).

Assemblage Structure

Nonmetric multidimensional scaling analysis indicated clear differences in assemblage structure between day and night samples (Figure 3). The NMDS analysis yielded two dimensions in assemblage space, with a stress value of 16.47, indicating that the ordination was good with a low chance of misrepresentation. Assemblage structure was significantly related to diel sampling period (ANOSIM: $R = 0.519$, $P < 0.01$) and was not significantly different among sandbank locations (ANOSIM: $R = 0.061$, $P = 0.16$).

Cluster Analysis

The UPGMA cluster analysis identified two major groups based almost entirely on day versus night samples (Figure 3). One day sample was contained within the predominantly nocturnal cluster, and three night samples fell within the predominantly diurnal cluster. These outliers were strongly influenced by the presence of small catfishes. The three nocturnal outliers (in the mainly diurnal cluster) were night samples taken early in the sample season (3 and 5 June 2008) before age-0 catfishes began to appear in samples, and the diurnal outlier (in the mainly nocturnal cluster) had a relatively high abundance of small catfishes (CPUE = 2.4).

DISCUSSION

Both the species richness and abundance of sandbank fish and shrimp assemblages were significantly greater in night samples than in day samples. Additionally, NMDS analysis indicated that assemblage structure was significantly different between day and night samples, and UPGMA cluster analysis indicated

TABLE 1. Percent occurrence of species among samples and percentage of the total sample abundance for day and night samples from the seven sandbanks in the Brazos River, Texas.

			Diurnal (n = 17)		Nocturnal (n = 18)	
Order	Family	Species	% samples present	% of total abundance	% samples present	% of total abundance
Atheriniformes	Atherinidae	Inland silverside *Menidia beryllina*	100	3.7	78	1.3
Clupeiformes	Clupeidae	Gizzard shad *Dorosoma cepedianum*	88	8.7	89	4.3
	Clupeidae	Threadfin shad *Dorosoma petenense*	29	1.2	67	2.6
	Clupeidae	Small *Dorosoma* spp.	24	6.7	22	1.4
Cypriniformes	Catostomidae	River carpsucker *Carpiodes carpio*	71	4.3	83	1.8
	Cyprinidae	Red shiner *Cyprinella lutrensis*	100	35.5	89	14.3
	Cyprinidae	Blacktail shiner *Cyprinella venusta*	6	<0.1	0	<0.1
	Cyprinidae	Shoal chub *Macrhybopsis hyostoma*	18	0.9	94	9.6
	Cyprinidae	Ghost shiner *Notropis buchanani*	94	4.9	89	2.6
	Cyprinidae	Bullhead minnow *Pimephales vigilax*	100	25.6	94	12.8
Cyprinodontiformes	Poeciliidae	Western mosquitofish *Gambusia affinis*	94	4.6	72	0.8
Decapoda	Palaemonidae	Ohio River shrimp *Macrobrachium ohione*	0	<0.1	56	1.4
Lepisosteiformes	Lepisosteidae	Alligator gar *Atractosteus spatula*	6	<0.1	0	<0.1
	Lepisosteidae	Longnose gar *Lepisosteus osseus*	76	1.1	61	0.3
Perciformes	Centrarchidae	Green sunfish *Lepomis cyanellus*	12	0.1	6	<0.1
	Centrarchidae	Bluegill *Lepomis macrochirus*	0	<0.1	6	<0.1
	Centrarchidae	Spotted bass *Micropterus punctulatus*	12	0.1	6	<0.1
	Centrarchidae	Largemouth bass *Micropterus salmoides*	53	0.6	39	0.2
	Centrarchidae	White crappie *Pomoxis annularis*	6	0.1	17	0.2
	Centrarchidae	Small *Lepomis* spp.	12	<0.1	17	0.1
	Moronidae	White bass *Morone chrysops*	12	0.1	22	0.1
	Mugilidae	Striped mullet *Mugil cephalus*	6	<0.1	22	0.1
	Percidae	Bluntnose darter *Etheostoma chlorosoma*	6	<0.1	0	<0.1
	Percidae	Dusky darter *Percina sciera*	18	0.1	6	<0.1
	Sciaenidae	Freshwater drum *Aplodinotus grunniens*	6	0.1	33	0.2
Siluriformes	Ictaluridae	Blue catfish *Ictalurus furcatus*	18	0.2	61	1.8
	Ictaluridae	Channel catfish *Ictalurus punctatus*	18	0.6	67	6.9
	Ictaluridae	Flathead catfish *Pylodictis olivaris*	0	<0.1	6	<0.1
	Ictaluridae	Small *Ictalurus* spp.	24	0.6	83	37.1

two major clusters based on differences between diurnal and nocturnal assemblage structure. Species richness, abundance CPUE, and assemblage structure did not differ significantly among the sandbank habitats.

Some of the variation between day and night samples can be influenced by differences in sampling efficiency if certain species can evade the seine more easily during the day than at night (Holland-Bartels and Dewey 1997). For example, striped mullet were more abundant on sandbanks at night. On several occasions, striped mullet were observed on sandbanks during the day but eluded capture. However, this is an unlikely explanation of the turnover in Ohio River shrimp and the many small fish species having slower swimming speeds, both of which accounted for most of the observed variation in diel assemblage structure.

In the Brazos River, we observed two behavioral groups: species that were both diurnally and nocturnally present on sandbanks (represented mostly by catostomids, clupeids, cyprinids, and poeciliids) and species that were almost entirely restricted to night samples (represented by ictalurids and palaemonids). The fishes that were consistently present on sandbanks were probably foraging during the day and resting in the shallow areas positioned high on sandbanks for refuge from predators at night. Shallow areas near the riverbank are associated with inshore hydraulic retention and thus probably have greater densities of benthic algae and phytoplankton than do deeper channel habitats (Schiemer et al. 2001). In the Brazos River, the complexity of woody debris patches is positively associated with macroinvertebrate abundance (Schneider and Winemiller 2008). However, cyprinids and some other small-bodied fish may not

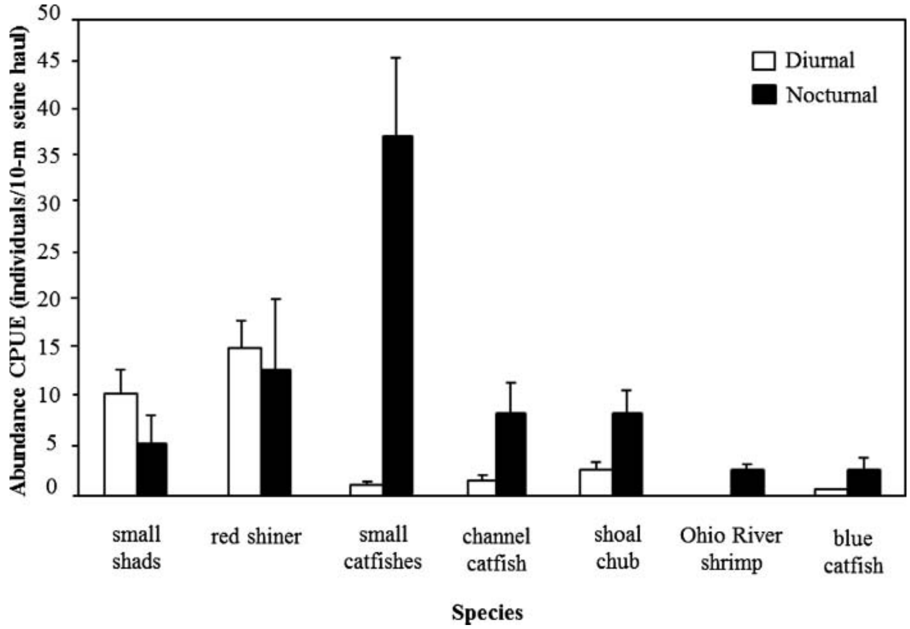

FIGURE 2. Taxa with the greatest diel differences in mean abundance CPUE. The two taxa on the left were common on sandbanks both during the day and at night, while the five taxa on the right were common on sandbanks only at night; both groups are presented in decreasing order of difference. Error bars indicate SEs.

be able to diurnally migrate to structurally complex habitats to feed on invertebrates because of an inability to tolerate fast current velocity (Yu and Peters 2002). Previous research in marine and freshwater ecosystems has documented a nocturnal migration of large fish predators to the shallow littoral zone to exploit the abundant diurnal fish that occur and remain inactive there (Sanders 1992; Copp and Jurajda 1993; Borcherding et al. 2002). In the Brazos River, large predators include the alligator gar, blue catfish, channel catfish, flathead catfish, largemouth bass, longnose gar, spotted bass, spotted gar, white bass, and fishing birds (e.g., herons family Ardeidae and kingfishers family Cerylidae; Zeug et al. 2005; authors' personal observations).

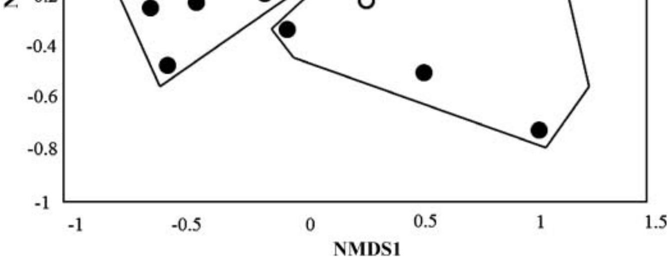

FIGURE 3. Nonmetric multidimensional scaling analysis (NMDS) of samples divided into two groups based on UPGMA cluster analysis.

Diel turnover of fish assemblage structure may be associated with diel changes in competitors, predators, and resource availability (Metcalfe et al. 1999; Kronfeld-Schor et al. 2001; Clark et al. 2003). Fishes that use sandbanks almost exclusively at night and Ohio River shrimp probably migrate to structurally complex habitats to escape predation during the day and return to shallow-water sandbanks to forage at night. During the daytime, juvenile blue and channel catfish seem to be associated with rocky shoals, riffles, or woody debris in the main channel (e.g., Wolter and Freyhof 2004), and Ohio River shrimp are associated with submerged leaf packs and woody debris (authors' personal observations). Longnose gars in this reach of the Brazos River prey heavily upon juvenile catfish (Robertson et al. 2008).

The use of shallow littoral habitats for both daytime feeding and nighttime resting by certain groups of fish and the nocturnal use of these habitats for foraging by other groups of fish seem to be general trends in freshwater ecosystems and may be associated with a tradeoff between predator avoidance and resource availability. For example, a study of the diel changeover of fish assemblages in the Cinaruco River, a species-rich blackwater river in Venezuela, documented that small-bodied characids were persistently abundant residents of sandbanks (Arrington and Winemiller 2003). Additionally, of the 134 species collected, 8 species were exclusively collected in day samples and 72 species were exclusively collected in night samples (Arrington and Winemiller 2003). Similar trends have also been documented in the Morava River, Czech Republic (Copp and Jurajda 1993), the Oder River, Germany (Wolter and Freyhof 2004), the Ohio and Muskingum rivers, USA (Sanders 1992), the Thames River, UK (Kubecka and Duncan 1998), and in some temperate reservoirs (Kubecka 1993).

Assessments of fish assemblage structure and habitat use are the foundation for models that attempt to predict how future environmental change will affect freshwater species. Niche models infer species' spatial distributions under alternative climate change scenarios based on relationships between species presence–absence and environmental variables (Elith and Leathwick 2009). In addition, physical habitat simulation models infer usable habitat area in streams based on relationships between patterns of species habitat use and hydrology, and these models are often used to predict the impacts of future water diversions (Xenopoulos and Lodge 2006) and for instream flow management (Spence and Hickley 2000). Both day and night samples are needed to obtain an accurate account of fish habitat use in order to develop predictive models for natural resource management.

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