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IMPORTANCE OF FLOODPLAIN CONNECTIVITY TO FISH POPULATIONS IN THE APALACHICOLA RIVER, FLORIDA

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ABSTRACT

Floodplain habitats provide critical spawning and rearing habitats for many large-river fishes. The paradigm that floodplains are essential habitats is often a key reason for restoring altered rivers to natural flow regimes. However, few studies have documented spatial and temporal utilization of floodplain habitats by adult fish of sport or commercial management interest or assessed obligatory access to floodplain habitats for species' persistence. In this study, we applied telemetry techniques to examine adult fish movements between floodplain and mainstem habitats, paired with intensive light trap sampling of larval fish in these same habitats, to assess the relationships between riverine flows and fish movement and spawning patterns in restored and unmodified floodplain distributaries of the Apalachicola River, Florida. Our intent is to inform resource managers on the relationships between the timing, magnitude and duration of flow events and fish spawning as part of river management actions. Our results demonstrate spawning by all study species in floodplain and mainstem river habitat types, apparent migratory movements of some species between these habitats, and distinct spawning events for each study species on the basis of fish movement patterns and light trap catches. Additionally, *Micropterus* spp., *Lepomis* spp. and, to a lesser degree, *Minytrema melanops* used floodplain channel habitat that was experimentally reconnected to the mainstem within a few weeks of completing the restoration. This result is of interest to managers assessing restoration activities to reconnect these habitats as part of riverine restoration programmes globally.

KEY WORDS: river; floodplain; spawning; seasonal flooding

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INTRODUCTION

The role of large-river floodplains and their relevance to the physical features and ecology of mainstem river systems is a major theme in riverine ecology (Gunderson, 1968; Wharton *et al*., 1982; Welcomme, 1995; Tockner *et al*., 1998). Floodplains generally accumulate and store nutrients during low-flow seasons and release these nutrients into mainstem river systems during high flows, thus providing much of the primary production that supports these aquatic ecosystems (Junk *et al*., 1989). Floodplains also help mitigate the impacts of seasonal flood events by dispersing increased amounts of water over large spatial areas (Walbridge, 1993). Additionally, floodplains are thought to play an important role in the life stages of many lotic fish species including those that support large commercial and recreational fisheries. Floodplain channels are the main source and path of rivers supplying water to the seasonally inundated floodplains and typically contain water even when floodplains are dry. Some fish species may use floodplain channel systems as corridors to spawning grounds during high water flow periods, and juvenile fish may utilize floodplains and their associated complex habitats as nursery grounds (Shaeffer & Nickum, 1986; Copp, 1989). Seasonal inundations of floodplains are postulated to increase plant production and animal diversity in the river-floodplain ecosystem (Junk *et al*., 1989), and seasonal floodplain inundation has been linked with the increased yield of fishes in riverine systems (Bayley, 1991; Agostinho & Zalewski, 1995).

Altering the natural flow regime of fluvial systems through flow control via dams and levees may cause changes in the channel characteristics and hydrology of both the mainstem river and floodplain habitats. These changes may affect fish communities by deepening the mainstem channel, leading to decreased floodplain inundation or complete disconnection of a floodplain channel from its associated mainstem river channel (Ligon *et al*., 1995; Light *et al*., 2006). This process may ultimately result in limiting fish access to floodplain habitats. Changes in the natural flow regimes of rivers and alterations to the floodplain channel–mainstem connectivity may lead to decreased diversity and production of fishes in a variety of river ecosystems (Bayley, 1995; Grift *et al*., 2001). In addition, materials that provide fish habitat in river channels, such as large wood, are frequently derived

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from floodplain habitats (Collins & Montgomery, 2002). Disruption of connections between a river and its floodplain channel may impact fish communities by disrupting food or spawning and rearing resources required by riverine fish populations.

In Europe, North America and northern Asia, 71% of large rivers are affected by the installation of dams, dikes and levees (Dynesius & Nilsson, 1994), all of which have altered the natural flow patterns of these systems (Sparks, 1995; Tockner & Schiemer, 1997; Galat *et al*., 1998). Regulated river ecosystems have been historically managed to control the timing, duration and magnitude of water flows, often to protect human interests downstream. Recently, restoration plans for many lotic ecosystems in Europe (Danube and Rhine rivers) and in the USA (Kissimmee and lower Mississippi rivers) have focused on re-establishing the natural flow regimes of modified systems (Zsuffa & Bogardi, 1995) to improve the connectivity of floodplains to the mainstem river and control the intensity and duration of flooding (Dahm *et al*., 1995; Heiler *et al*., 1995; Toth *et al*., 1995; Tockner & Schiemer, 1997; Buijse *et al*., 2002). Ecological benefits of natural flow regimes are often based on the idea that natural flow conditions maximize the ability of native species to fill available ecological niches (Bayley, 1995; Poff *et al*., 1997). Although improved connectivity between mainstem and floodplain habitats and increased inundation of floodplains has been shown to enhance some fish populations (Rood *et al*., 2003), and evidence suggests the importance of floodplain habitat to groups of lotic fish species (Agostinho *et al*., 2001), few studies have examined the spatiotemporal use of floodplain channel habitats by adult fishes and correlated this use with spawning behaviour. This represents an under-studied aspect of floodplain channel–mainstem connectivity that may provide guidance to management agencies charged with making decisions related to restoring lotic systems.

As demand for water resources increases, the costs of managing flows to maintain floodplain habitats required by fishes as spawning and nursery habitats is countered by the loss of benefits to humans for reservoir storage and decreased water availability. Understanding the interaction between floodplain channel and mainstem rivers and the fish communities associated with these systems is a critical component in implementing effective management policies. A major concern in managing reservoir releases in the southeastern US is the timing, magnitude and duration of seasonal flow events that are thought to offer critical spawning cues and juvenile rearing habitats for lotic fish species. However, this conceptual model has not been extensively validated.

We investigated the importance of floodplain channel–mainstem connectivity to fish populations in the Apalachicola River, Florida, by comparing adult fish movements with larval fish collections in the mainstem Apalachicola River and two floodplain channel systems, River Styx and Battle Bend. We focused on the following objectives: (i) to determine spatial and temporal movement patterns of adult fishes in both mainstem and floodplain channel systems; (ii) to examine correlations of temporal habitat used by adult fishes with spawning events and environmental conditions inferred from larval fish collections in the mainstem and floodplain channels; and (iii) to determine if mainstem and floodplain fish populations are independent or linked on the basis of results of the first two study objectives. Addressing these objectives will improve the understanding of adult fish movement patterns in mainstem and floodplain habitats and how these movement patterns relate to fish spawning and flow conditions. This would aid resource managers in their ability to develop effective flow policies to protect fish resources and minimize costs to human users associated with water releases.

STUDY SITE

The Apalachicola River is formed by the confluence of the Flint and Chattahoochee Rivers in southwestern Georgia; combined, all three rivers (commonly referred to as the ACF basin) have a drainage area of 50 700 km^2 in Alabama, Georgia and Florida (Figure 1). The Apalachicola River has the largest discharge of all rivers in Florida (Iseri & Langbein, 1974). Flow in the Apalachicola River is currently the focus of a water allocation dispute between the three states in which the basin lies, representing one of the most contentious and litigated water disputes in the eastern United States. More than 320 km of floodplain sloughs, streams and lakes occur along the non-tidal reach of the Apalachicola River, and these habitats are used by approximately 80% of fish species in this system (Light *et al*., 1998). Impoundments and channel changes since the completion of Jim Woodruff Lock and Dam in 1954 have reduced flows to all of these floodplain systems, generally decreasing the amount of time annually that these habitats are accessible to fishes and reducing the interaction of floodplain outputs with the mainstem river (Light *et al*., 2006).

This study focused on an area in the non-tidal lower reach of the Apalachicola River including the mainstem Apalachicola River and two adjacent floodplain systems along the east bank of the mainstem: River Styx and Battle Bend (Figure 1). River Styx enters the Apalachicola River at river kilometre (RKM) 56.9 and is a relatively undisturbed tributary floodplain system that is connected to the mainstem by a series of seasonal and perennial sloughs. When mainstem Apalachicola River flows are approximately 227 m^3/s, River Styx acts much like a lake with slow moving water. As flows in the mainstem of the Apalachicola River increase to

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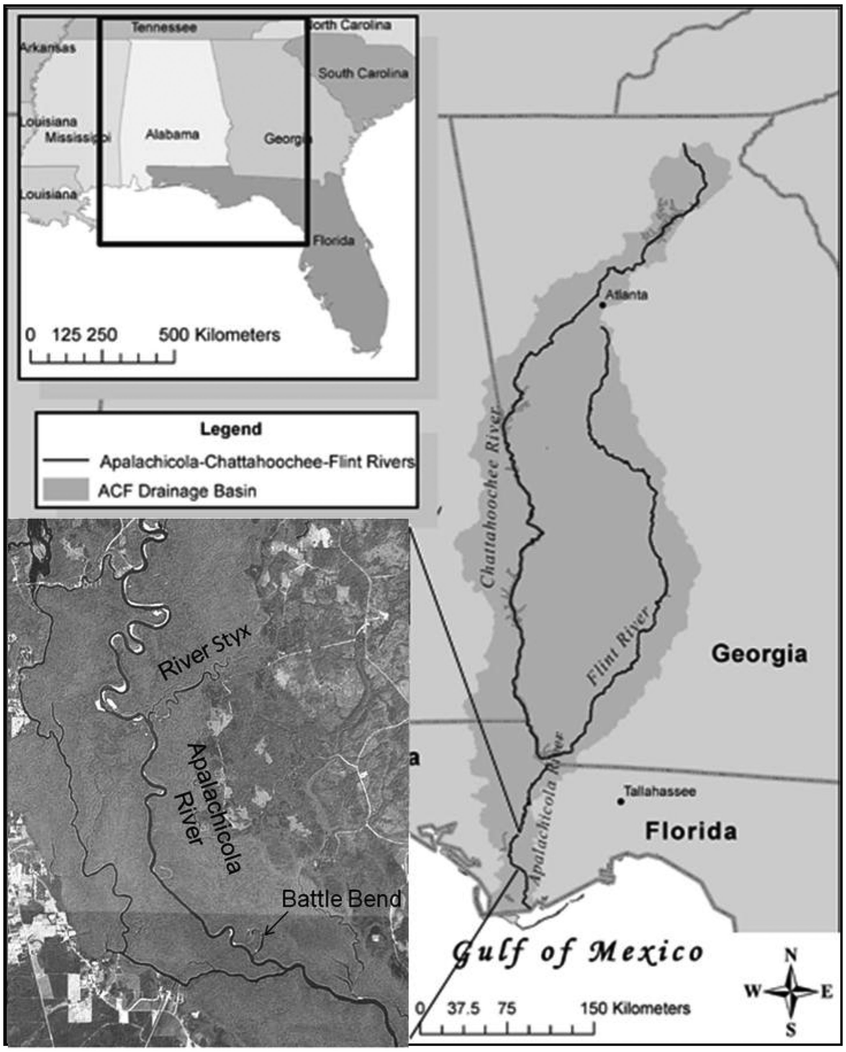

Figure 1. Map of the Apalachicola–Chattahoochee–Flint River drainage basin.

medium-high flows (approximately 765 m^3/s), increased flow from connecting sloughs, creeks and streams move through this upper swamp corridor as sheetflow (Light *et al*., 1998).

Experimental floodplain reconnection

Battle Bend (RKM 46.3) is a floodplain oxbow lake that was created in 1969 by the US Army Corps of Engineers (USACE) as part of a series of meander and bend easements for navigation purposes (USACE, 1986) in the Apalachicola River. After this meander was cut off, Battle Bend was disconnected from the Apalachicola River at flows below 255 m^3/s (Light *et al*., 1998). In an effort to restore connectivity of Battle Bend with the mainstem Apalachicola River at lower water levels, approximately 49 000 m^3 of sediment and debris that had been deposited at the mouth of Battle Bend subsequent to the bend easing project was removed during fall of 2006. These efforts were part of a restoration project to provide fish passage and connectivity between the mainstem Battle Bend at water levels $<$255 m^3/s (C. Mesing, Florida Fish and Wildlife Conservation Commission, personal communication). The expectation was that by removing debris and sediments blocking fish passage, fishes, including those of commercial and recreational value, may once again use this historically accessible spawning habitat and nursery ground, possibly improving the viability of these fish populations.

METHODS

Study species

Fish study species were selected with the assistance of the Florida Fish and Wildlife Conservation Commission to represent a range of species that have either a fishery value

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(i.e. largemouth bass, *Micropterus salmoides*; spotted bass, *Micropterus punctulatus*; channel catfish, *Ictalurus punctatus*; redear sunfish, *Lepomis microlophus*) or represent a species guild known to primarily live in large rivers (i.e. spotted sucker, *Minytrema melanops*).

Tagging and telemetry

Beginning in March 2006, 39 Vemco® sonic telemetry tags (Vemco Ltd., Halifax, Nova Scotia, Canada) and 41 ATS (R) radio tags (ATS Inc., Isanti, MN, USA) were surgically implanted in largemouth bass, spotted bass, spotted suckers and redear sunfish. A 10–15-mm incision was made immediately lateral of the ventral side of the body between the pelvic fins and the anal fin, exposing the body cavity. The telemetry tag was inserted into the body cavity and positioned posteriorly. The incision site was closed with two to three sutures, depending on incision length, using a 3/0, 24-mm cutting needle fitted with polydioxanone monofilament synthetic absorbable suture material (CP Medical Inc., Portland, OR, USA). The minimum guaranteed battery life of tags ranged from 130 days for small tags implanted in redear sunfish and spotted suckers to 180 days for larger tags implanted in largemouth bass, spotted bass and later channel catfish. All telemetry tagged fish were also marked with an external T-bar anchor tag (Hallprint Pty Ltd., Crescent, Hindmarsh Valley, South Australia) with an identification number, telephone number and a message to release the fish. Fish were tagged and released in both the mainstem of the Apalachicola River and in River Styx through a staggered-entry design to maximize monitoring time of each species as related to the battery life of the tags.

In December 2006, 120 Vemco® sonic telemetry tags were surgically implanted in the same species as aforementioned plus channel catfish generally following the same procedures (Burgess, 2008). In this year, fish were tagged and released in the mainstem of the Apalachicola River and in Battle Bend, which had recently been reconnected to the mainstem river as part of the habitat enhancement project described previously.

Arrays of passive, autonomous, acoustic receivers (VR2, Vemco Ltd., Halifax, Nova Scotia, Canada) were deployed in River Styx, the mainstem of the Apalachicola River, and in sloughs connecting these systems for the first year of the study (March to December 2006). Additional receivers were added to the Battle Bend region after debris removal and channelization was completed during the second year (December 2006 to December 2007). Passive receivers recorded date, time and tag number of telemetered fish when the tagged fish were within the reception range of the receivers. Preliminary range testing indicated that passive receivers were able to detect tagged fish up to 150 m from a receiver when there were no obstructions. VR2 receivers were checked, and data were downloaded twice per month during the monitoring periods.

Two active tracking methods were employed to capture movement data. The first method used a unidirectional hydrophone, and a receiver deployed from randomly chosen starting points within the study site to track fish with sonic telemetry tags (active tracking). The second method, termed a ‘tag sweep’, was only used to locate tagged fish during the second year of the study (2007). To sweep the entire study site, people in two boats actively tracked by starting at opposite ends of the study site and each boat moved towards the other vessel and stopped approximately every 300 m (average detection distance with the manual tracking receiver and hydrophone) at one of 125 pre-designated monitoring sites. At each monitoring station, the hydrophone was used to check for the presence of tagged fish, and if tagged fish were located, the signal was attenuated until the most precise location was determined, and the position was then recorded via global positioning system (Burgess, 2008). A simultaneous project in the region of this study on the Apalachicola River was in progress that monitored tagged fish from the estuarine region up to Jim Woodruff Lock and Dam (upstream migration barrier). This project used the same passive and active tracking techniques ensuring that any tagged fish migrating from the study site would be detected.

Seasonal habitat use

Seasonal use of the floodplain channel and mainstem river (referred to as habitats) by telemetered adult fish was determined by examining the temporal changes in habitat use by different species on the basis of detections (both passive and active tracking detections). Seasonal habitat use was assessed for individual species on a monthly time scale. The habitat use by individual species was determined as a function of the number of detections in a given habitat and the total number of detections in all habitats during a given month:

$$H_{i,j} = \frac{n_{i,j}}{\sum_i n_j} \tag{1}$$

where $H_{i,j}$ is the proportion of *i* habitat use by species *j* during a given month and $n_{i,j}$ is the number of detections in *i* habitat by species *j* during a given month.

This method of calculating habitat use assumed that (i) the frequency of tag signals (pings) was equal for all individuals, (ii) the probability of detecting each individual tagged fish was the same and (iii) the probability of detection in each habitat was the same. Assumption one was reasonable because each species received a tag with the same pinging frequency. Assumption two basically assumes the tagged individuals represent the species as a whole. Assumption three was met by arranging the receiver arrays as ‘gates’ that existed in transition zones between floodplain habitats and the main river channel such that the detection range of gate receivers

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covered the entire area between both banks of the transition zone. This resulted in a high degree of certainty when an individual fish passed through the transition zone (i.e. when fish changed habitats).

Individual fish were separated into groups on the basis of whether they used both mainstem river and floodplain channel habitat or only one habitat type. Per cent of individuals within each species using only one habitat type or both habitat types were calculated to provide insight into proportion of individuals within a species that display migratory versus non-migratory movement patterns. Maximum linear ranges of individuals (river distance between most upstream and most downstream detection) were also separated and were used to calculate mean individual maximum linear ranges for individuals of each species based upon this habitat use criteria.

Home range estimation

Kernel density estimates were calculated using ArcView© GIS version 3.3 (HCL Technologies Ltd., New Delhi, India) with the Animal Movements Analyst Extension (Hooge *et al*., 1999) to determine the home ranges of adult fishes during the study period. These kernel home ranges were determined for individual fish from a set of telemetry points from the receiver array to create density estimates and were interpreted as a utilization distribution (UD; Van Winkle, 1975). A minimum number of 15 independent detections for each individual were required to produce reasonable home range estimates. Independent detections were determined by using only one detection per receiver per day, termed 'day hits'. Using the day hit method satisfied the assumptions of independent detections by avoiding autocorrelated events. In addition, the least squares cross validation method was used to choose the optimum kernel density bandwidth, h (smoothing parameter). The kernel bandwidth determined the influence of observations on the density estimate, such that narrow bandwidths allowed greater influence of nearby observations, and wide bandwidths allowed for greater influence by more distant observations (Seaman and Powell, 1996).

We also calculated the kernel density estimates by using the lowest cost path distance metric (Jensen *et al*., 2006) that were bound to the river by a raster file. This tool ensured that calculations were made using only water distance and did not cover land as was necessary in a sinuous river such as the Apalachicola River.

We used the detection data and a binomial likelihood to estimate the probability of the telemetered fish using each habitat type through the spawning season:

$$L(\Psi|x) = \binom{s}{x} \Psi^{x}(1-\Psi)^{s-x} \tag{2}$$

where Ψ is occupancy, x is either 1 or 0 depending on presence or absence in the habitat, s is the number of sites and $L(\Psi|x)$ is the likelihood of Ψ given the data x.

This model of habitat use was a modification of the basic occupancy model from MacKenzie *et al*. (2005) by using presence/absence data input from our telemetry relocations within our array on a daily time scale and maximizing the likelihood by using Microsoft® Office Excel's solver on a weekly scale to assign a probability of how likely a fish was to be found in either the floodplain or mainstem habitat in a given week. This habitat use model has slightly different assumptions compared with occupancy models. Occupancy assumes that (i) sites are closed to changes in Ψ and (ii) Ψ is constant across sites or modelled as a covariate. This application defines changes in Ψ through time as the probability of habitat use. Occupancy assumes that (iii) the detection of species and detection histories are independent. Our habitat use application satisfies this assumption by using 'day hits' for independent detections. Finally, occupancy assumes that (iv) there is no unmodelled heterogeneity in detection probability. By using telemetry detections, we assume perfect detection probability by the passive receivers. This likelihood allowed us to assign a probability to species using a single habitat through time, which facilitated associations between habitat use, riverine flow conditions and occurrence of larval fish.

Larval fish collection

Larval fish collection followed the protocol established by the US Geological Survey as part of previous studies from 2002–2004 (Walsh *et al*., 2009) using a floating light trap based on a quatrefoil trap (Floyd *et al*., 1984; Kissick, 1993) to collect larval, postlarval and early juvenile fishes. Each night of light trap sampling consisted of deploying seven traps in the mainstem river and seven traps in the floodplain channel. Fish and invertebrates were retrieved via a collection bag (350-μm mesh) affixed to an open polyvinyl chloride ring at the trap bottom. Contents of each trap were fixed in 4% buffered formalin (Lavenberg *et al*., 1984) and returned to the laboratory. Traps were soaked for a minimum of 12 h using a battery operated submersible light. In the laboratory, specimens were transferred through an ethanol series for final storage, and larval and postlarval fish were identified to the lowest practicable taxonomic category and were measured (TL, mm) (Burgess, 2008; Walsh *et al*., 2009).

Determining spawn timing

Timing and duration of fish spawning in the floodplain and mainstem habitats were determined using plots of light trap catches of larval fish by date in each habitat type. Mean daily discharge of the Apalachicola River as measured at the USACE gauge near Blountstown (as in Walsh *et al*., 2009)

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was used in plotting discharge versus other parameters. This gauge was used to reduce the 'lag-time' in measured flows between other gauges (i.e. Chattahoochee) and our study sites given the interest in relating riverine conditions to fish behaviours on a restricted spatial and temporal scale. Lists of all taxa collected and their respective percent composition of catch are provided in Walsh *et al*. (2009). We constructed three-way plots for *Micropterus* spp. to show larval catch, river discharge and the probability of an adult telemetered *Micropterus* spp. being present in either the mainstem or floodplain habitat. On the basis of the samples examined, these three-way plots provided a snapshot of timing and duration of adult fish movement patterns, larval fish collections and riverine discharge across a common time period. Probability of habitat use functions were not calculated for other species because of smaller sample sizes and less frequent detections (see Discussion section). For other genera, we created two-way plots of larval catch and river discharge through time for the mainstem and floodplain habitats for each year.

RESULTS

General movement patterns

All fish tagged both in 2006 and 2007 were detected at least once after release. If the tagged fish did not move after repeated detections, the tag was censored and the fish assumed to have died or shed the tag (Burgess, 2008). We evaluated movement patterns of individual telemetered fish by classifying each fish as having used mainstem habitat only, floodplain channel only or both habitats (Table I). We found high fidelity to habitat type for some species (redear sunfish, channel catfish) and extensive movement between habitat types for other species (spotted sucker and largemouth bass). We found that for all species, the mean individual maximum range of each species using only floodplain channel habitat (floodplain only residents) was smaller than the mean range of individuals using both habitats (migratory individuals) (Table II). This trend occurred during both years. We also found that all mainstem only residents had a greater mean range of movement than did floodplain channel only residents for all species except redear sunfish. Additionally, with the exception of *Micropterus* spp. during 2006, the mean maximum linear range of individuals for each species that used both habitats was larger than that of individuals that used either mainstem habitat only or floodplain channel habitat only. A variety of community metrics for larval fish are available in Walsh *et al*. (2009). Species or genus specific results related to movements, habitat use and larval fish catches follow.

Lepomis spp.. Redear sunfish demonstrated movements between mainstem and floodplain habitats related to spawning season (Table I, Figure 2). Redear sunfish were primarily detected in floodplain habitats (Figure 2) from late spring through summer (April through August), and peak mainstem detections occurred during winter (December and January). Redear sunfish also had small linear movements and UD estimates generally suggesting restricted movements (Tables II and III). Less than 50% of the tagged redear sunfish used both mainstem and floodplain habitats; thus, their residency in either habitat singularly were highest among study species (Table II). This high residency and small number of tagged fish precluded our ability to estimate the probability a fish was in a given habitat for a particular day.

Table I. Per cent of individuals of each tagged species that used only mainstem habitat, only floodplain channel habitat or both habitats over the entire field season

		Per cent habitat use			
	Species	Mainstem only	Floodplain only	Both	*N*
(2006) River Styx focus					
	Redear sunfish	17	66	17	6
	Largemouth bass	36	37	27	11
	Spotted bass	44	11	45	9
	Spotted sucker	0	38	62	8
	Channel catfish	—	—	—	0
(2007) Battle Bend focus					
	Redear sunfish	26	35	39	23
	Largemouth bass	31	17	52	23
	Spotted bass	20	20	60	5
	Spotted sucker	12	28	60	25
	Channel catfish	63	0	37	24

New individuals were tagged during 2007.

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Table II. Mean individual maximum range ±1 standard deviation of tagged species that used only mainstem habitat, only floodplain channel habitat or both habitats over the entire field season

		Mean range (km) by habitat use		
	Species	Mainstem only	Floodplain only	Both
(2006) River Styx focus				
	Redear sunfish	$<0.01 \pm 0.00$	1.22 ± 7.37	14.23 ± 0.00[a]
	Largemouth bass	2.98 ± 1.35	0.92 ± 0.88	2.12 ± 1.51
	Spotted bass	10.03 ± 0.00	2.89 ± 0.00	6.57 ± 3.41
	Spotted sucker	—	2.31 ± 2.70	13.14 ± 13.22
	Channel catfish	—	—	—
(2007) Battle Bend focus				
	Redear sunfish	0.05 ± 0.10	0.29 ± 0.31	3.26 ± 4.07
	Largemouth bass	4.04 ± 3.73	1.89 ± 1.99	5.76 ± 8.38
	Spotted bass	2.49 ± 0.00	1.33 ± 0.00	3.37 ± 1.67
	Spotted sucker	28.64 ± 48.84	0.37 ± 0.35	28.83 ± 37.26
	Channel catfish	5.67 ± 4.95	—	16.87 ± 13.95

New individuals were tagged in 2007.
[a]Represents only one redear sunfish; value may indicate a possible anomaly.

Light trap catches of larval *Lepomis* spp. were only identifiable to genus for some individuals primarily because of uncertainty in identifying redear sunfish. However, most larval *Lepomis* that were identifiable were bluegill sunfish, *Lepomis macrochirus*. On the basis of our light trap catches, larval *Lepomis* were generally collected in the floodplain habitats before they were collected in the mainstem habitat (Figure 3) suggesting spawning occurred earlier in the year in floodplain than mainstem habitats. Light trap samples first collected larval *Lepomis* in the floodplain generally in mid-March and in the mainstem about a month later (Figures 3 and 4) and continued through July when sampling ended. Additionally, a greater proportion of the floodplain light trap samples contained larval *Lepomis* than mainstem in both years (Figures 3 and 4). *Lepomis* spp. were documented spawning in the newly reconnected Battle Bend floodplain in the first spawning season following restoration of connectivity to the mainstem river.

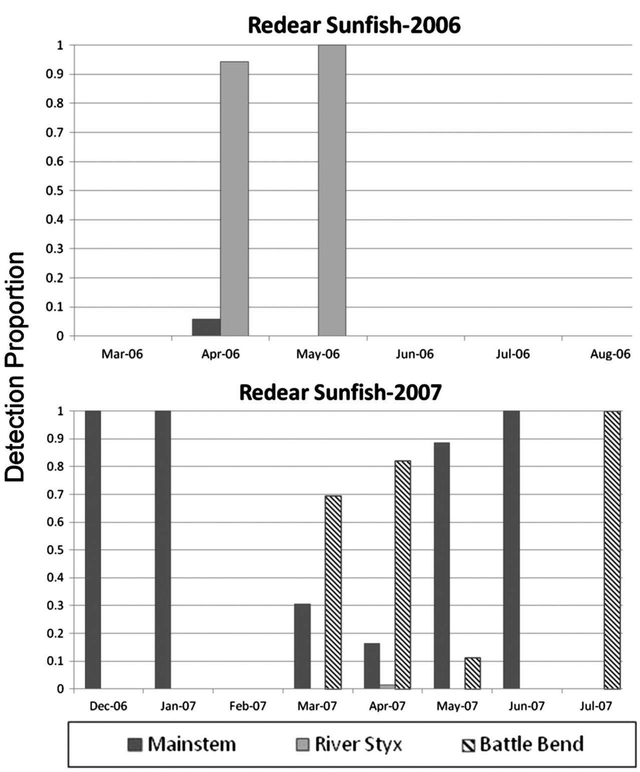

Figure 2. Proportion of detections (y-axis) of redear sunfish during 2006 and 2007 in the mainstem of the Apalachicola River (black bars), River Styx (grey bars) and Battle Bend (diagonal bars) as monthly proportions.

Minytrema melanops. Spotted sucker movement patterns were dynamic as about 60% of tagged fish used both mainstem and floodplain habitats in each year (Table I). Spotted sucker also demonstrated the largest mean individual range (Table II) and some of the largest home range UD of species studied in each year (Table III). We were unable to estimate probability of movement between mainstem and floodplain habitat for spotted sucker, likely because infrequent movement between the mainstem or floodplain habitats reduced observations of the "transition" between habitat types. Spotted sucker movement patterns from mainstem to floodplain habitats appear to have occurred prior to spawning (Figure 5). Spawning in the mainstem and floodplain habitats (as evidenced by light trap catches of spotted sucker) occurred at about the same time in both habitats each year (Figures 6 and 7), and the Battle Bend floodplain habitat had a lower proportion of light traps that captured spotted sucker larvae. Spawning duration based on light trap catches appears to have been shorter for spotted sucker than other species, as light trap catches

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Table III. Mean individual home range utilization distribution (95% and 50%) ±1 standard deviation of tagged species for the 2006 and 2007 field seasons calculated by the Lowest Cost Path Script

	Species	Mean home range UD 95% (hectares)	Mean home range UD 50% (hectares)	N
(2006) River Styx focus				
	Redear sunfish	3.32 ± 0.00	1.15 ± 0.00	1
	Largemouth bass	2.87 ± 1.79	0.99 ± 0.59	3
	Spotted bass	24.22 ± 22.24	6.94 ± 4.89	6
	Spotted sucker	25.36 ± 31.12	7.87 ± 9.46	2
	Channel catfish	—	—	0
(2007) Battle Bend focus				
	Redear sunfish	8.05 ± 3.65	2.46 ± 1.04	7
	Largemouth bass	33.08 ± 46.04	7.69 ± 8.45	14
	Spotted bass	7.40 ± 8.60	2.80 ± 3.10	2
	Spotted sucker	21.91 ± 33.58	7.90 ± 13.73	14
	Channel catfish	43.98 ± 59.93	12.96 ± 16.71	7

New individuals were tagged in 2007.
UD, utilization distribution.

containing spotted suckers were generally found from mid-March until late May (Figures 6 and 7).

Micropterus spp.. Spotted bass and largemouth bass showed similar movement patterns between the mainstem and floodplain habitats with a high proportion of fish from both species using both habitat types (Table I; Figures 8 and 9). Maximum movement range and home range for both species were variable within a year between species and within a species between years, highlighting the large variation in individual behaviours and movements for these species (Tables II and III). Because of the frequency of detection of individual fish and the larger number of tagged *Micropterus* species (due to agency interest in managing this species), we were able to estimate the probability of a *Micropterus* being found in the mainstem or floodplain habitat. In general, movement patterns suggested that spotted bass and largemouth bass moved to the floodplain habitats prior to spawning (Figures 10 and 11). The probability that adult *Micropterus* spp. implanted with acoustic tags used floodplain habitat ranged from 0.67 to 1.0 during the spring (Figure 10) with two peaks in probability occurring in mid-March and also mid-April (probability = 95%–97%; Figure 10). The initial peak in

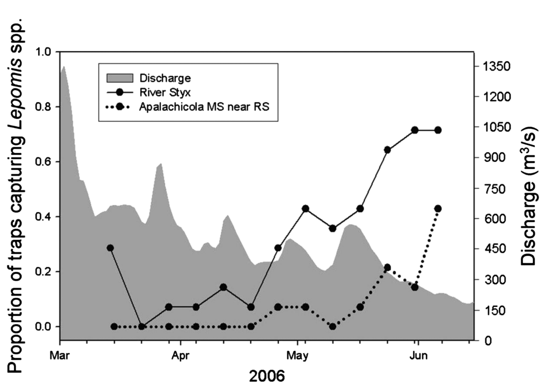

Figure 3. Plot of light trap catch (primary *y*-axis) and discharge (secondary *y*-axis) for *Lepomis* spp. in 2006. MS, mainstem; RS, River Styx.

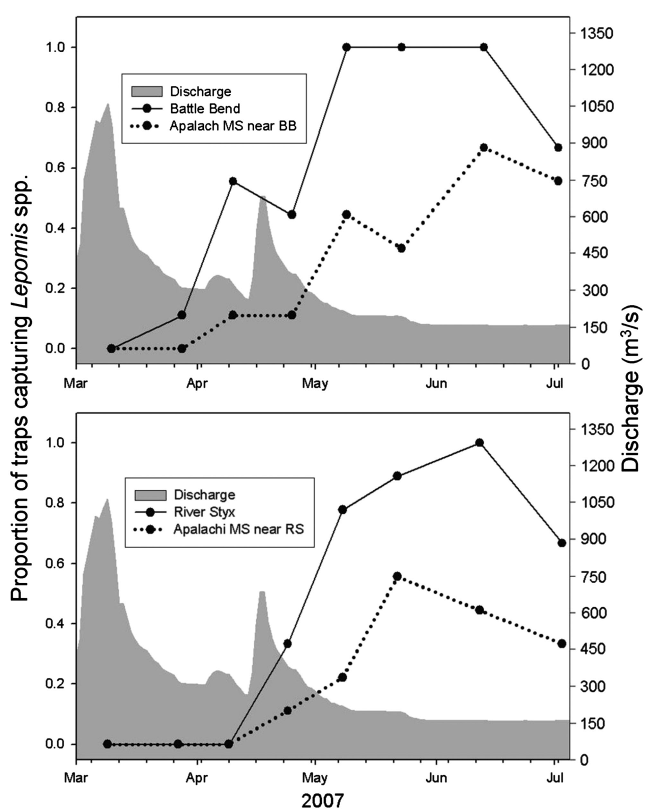

Figure 4. Plots of light trap catch (primary *y*-axis) and discharge (secondary *y*-axis) for *Lepomis* spp. during 2007. MS, mainstem; RS, River Styx; BB, Battle Bend.

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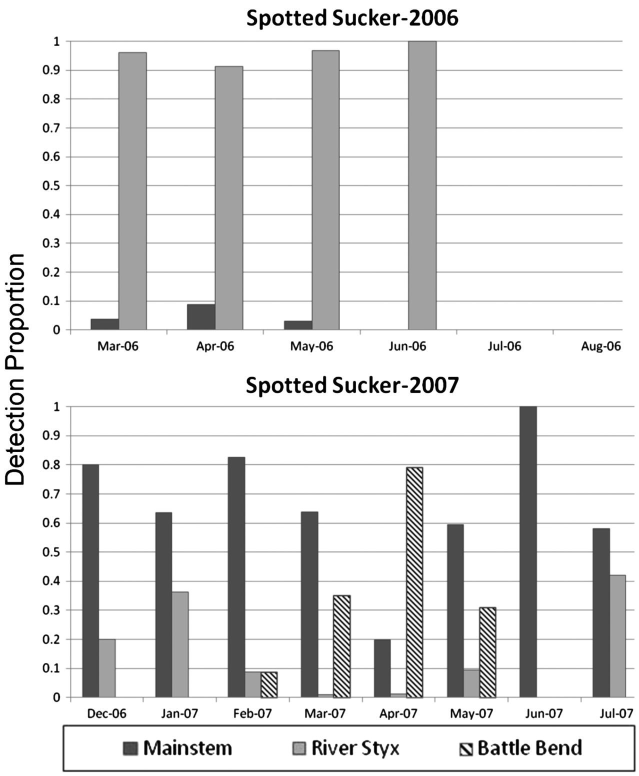

Figure 5. Proportions of detections of spotted sucker during 2006 and 2007 in the mainstem of the Apalachicola River (black bars), River Styx (grey bars) and Battle Bend (diagonal bars) as monthly proportions.

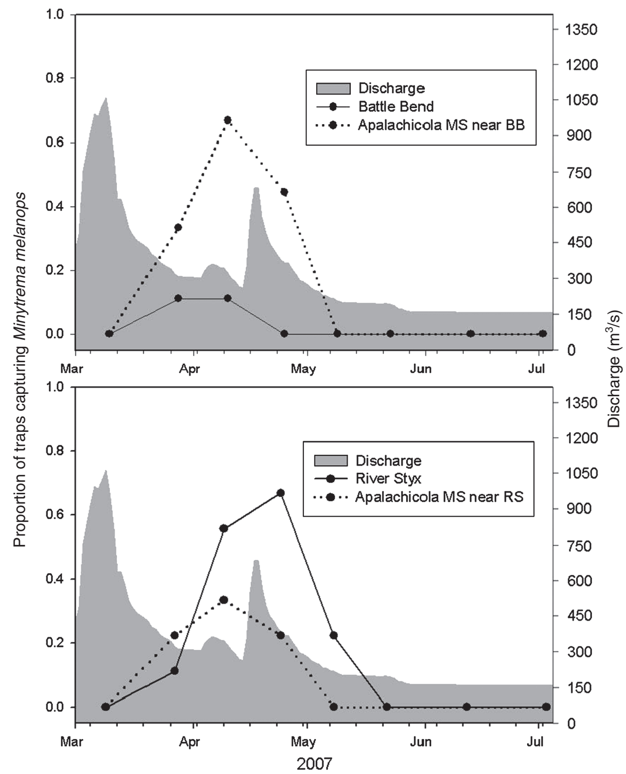

Figure 7. Plots of light trap catch (primary *y*-axis) and discharge (secondary *y*-axis) for *Minytrema melanops* in 2007. MS, mainstem; RS, River Styx; BB, Battle Bend.

adult *Micropterus* spp. habitat use preceded the appearance of larval *Micropterus* spp. among light trap collections (not identifiable to species) by approximately 2 weeks, and the secondary peak in adult *Micropterus* spp. floodplain habitat use (probability = 86%–97%) generally coincided with peak larval *Micropterus* spp. catch throughout April (Figure 10). Similar patterns were observed both in 2006 and 2007 (Figure 11) with peaks in probability of floodplain habitat use occurring in mid-April followed by the first captures of larval *Micropterus* spp. in the light traps about 2 weeks later (Figure 11).

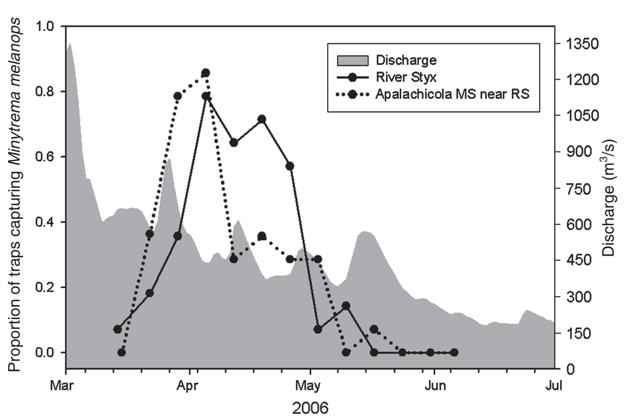

Figure 6. Plot of light trap catch (primary *y*-axis) and discharge (secondary *y*-axis) for *Minytema melanops* in 2006. MS, mainstem; RS, River Styx.

The probability that adult *Micropterus* spp. implanted with acoustic tags used floodplain habitat during spring of 2007 ranged from 0.30 to 0.91. As in 2006, this pattern showed greatest use of floodplain habitats by adult *Micropterus* spp. during the 2007 spawning period (Figure 11). In 2007, peak use of floodplain habitats by adult *Micropterus* spp. (about 90%) occurred from April 15 to 29 (Figure 11). We observed a lesser peak in floodplain habitat use by adult *Micropterus* spp. (74%) on March 11, which preceded the appearance of larval *Micropterus* spp. among light trap collections by approximately 2 weeks (Figure 11). Overall, high use of floodplain habitats by adult *Micropterus* spp. coincided with catches of larval *Micropterus* spp. among light trap collections several weeks later.

Ictalurus punctatus. Channel catfish were found to primarily use mainstem habitats, or both mainstem and floodplain habitat, but none of our telemetered fish used only floodplain habitat (Tables I and II). Channel catfish were found to have large mean range of movements and home range values (Tables II and III). Channel catfish were detected in floodplain habitats with highest frequency in

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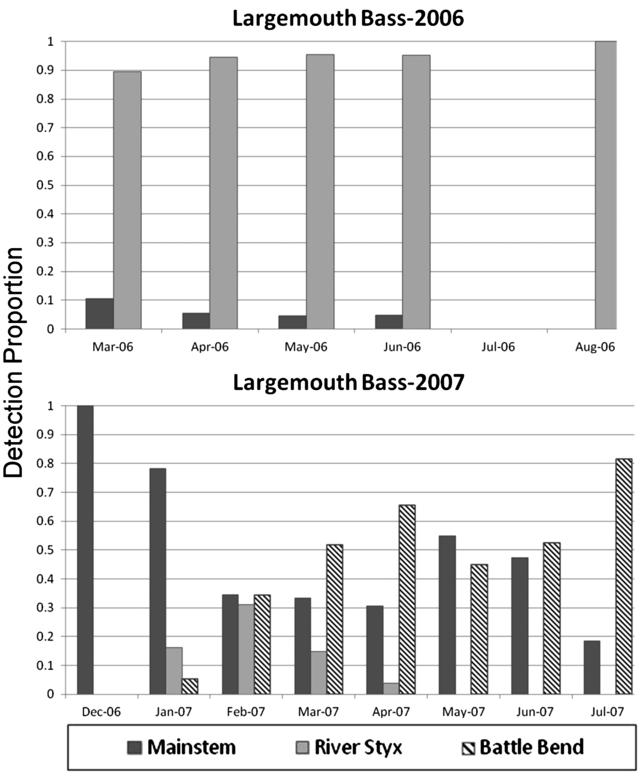

Figure 8. Proportion of detections of largemouth bass during 2006 and 2007 in the mainstem of the Apalachicola River (black bars), River Styx (grey bars) and Battle Bend (diagonal bars) as monthly proportions.

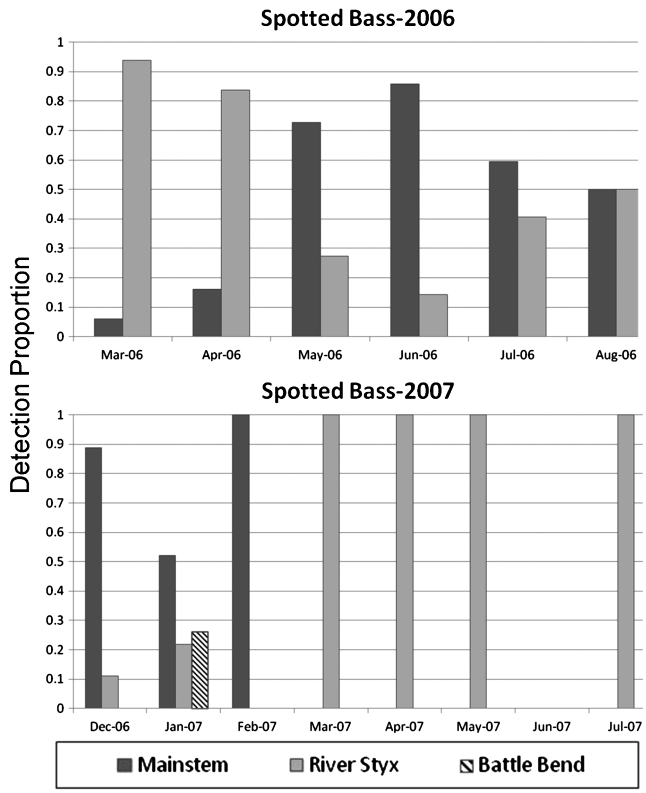

Figure 9. Proportion of detections of spotted bass during 2006 and 2007 in the mainstem of the Apalachicola River (black bars), River Styx (grey bars) and Battle Bend (diagonal bars) as monthly proportions.

March, and floodplain use decreased through May, after which channel catfish were only found in the mainstem Apalachicola River (Figure 12). Larval channel catfish were collected in very low numbers in light trap samples, presumably because larvae of this species may be negatively phototaxic, thus avoiding the light traps. Although channel catfish were not captured with sufficient frequency to assess the relationship between movement patterns, habitat use, and spawning, channel catfish movement into the mainstem occurred from about March through June, corresponding to the dates when water temperatures reached reported spawning temperature for this species (27 °C; late June). This suggests that although channel catfish may use both floodplain channel and mainstem river habitats, spawning may primarily occur in the mainstem.

DISCUSSION

Maintaining floodplain–mainstem river connectivity is thought to be an essential component of river restoration programmes to sustain primary production (Junk *et al*., 1989; Bayley, 1991; Gutreuter *et al*., 1999; Welcomme, 1995; Tockner *et al*., 1998), improve fish diversity and survival, and enhance growth rates of native fishes (Kwak, 1988; Matheney and Rabeni, 1995; Sommer *et al*., 2001). But, these connections can also facilitate invasions of non-native species to these habitats (Scheerer, 2002), reducing the effectiveness of floodplains as a refuge from non-native predators. Many riverine fish species use floodplain systems as spawning and rearing habitats, necessitating connectivity between floodplain and mainstem habitats. This connectivity allows movement between these habitats as part of ontogenetic habitat shifts (Shaeffer and Nickum, 1986; Kwak, 1988; Cañas and Pine, 2011). These conceptual ideas about the importance of floodplains to large-river ecosystems have made the study of these systems a major theme in riverine ecology (Gunderson, 1968; Welcomme, 1979; Wharton *et al*., 1982).

Seasonal movement patterns by adult fishes in the floodplain channel and mainstem river habitats indicated that at least part of the population of each studied species migrates between the mainstem and floodplain channel habitats. In 2006, there were individuals of each telemetered species that

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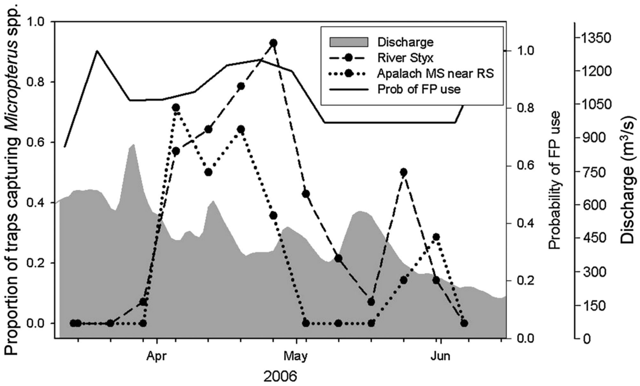

Figure 10. Plots of light trap catch (primary *y*-axis), probability of floodplain habitat use (secondary *y*-axis) and discharge (tertiary *y*-axis) for *Micropterus* spp. in 2006. MS, mainstem; RS, River Styx; FP, floodplain.

used both habitat types, but with the exception of spotted sucker, these proportions were lower than the values for 2007. Generally, in 2007, a greater proportion of each species used both habitat types than conspecifics that used only one habitat type. One exception was channel catfish that primarily used mainstem habitat only. Many of the behavioural differences between years for each species are likely explained by differences in the environmental conditions for

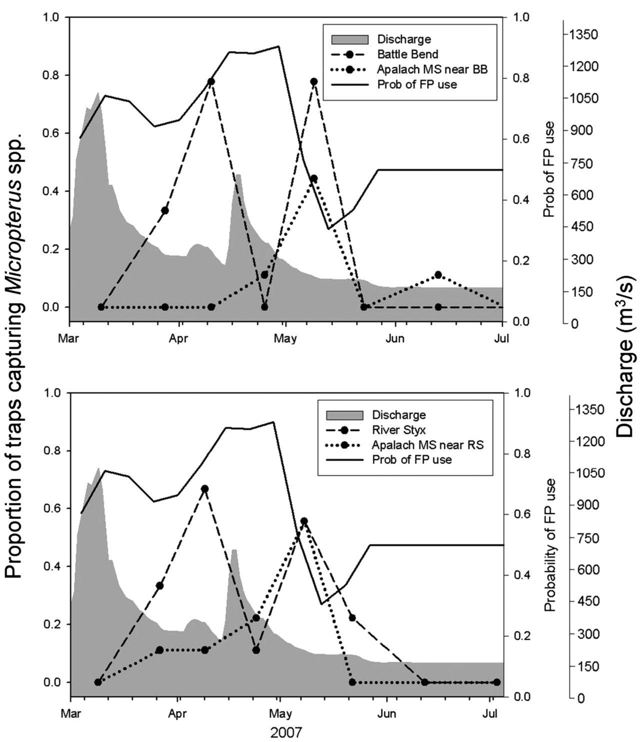

Figure 11. Plots of light trap catch (primary *y*-axis), probability of floodplain habitat use (secondary *y*-axis) and discharge (tertiary *y*-axis) for *Micropterus* spp. in 2007. MS, mainstem; RS, River Styx; BB, Battle Bend; FP, floodplain.

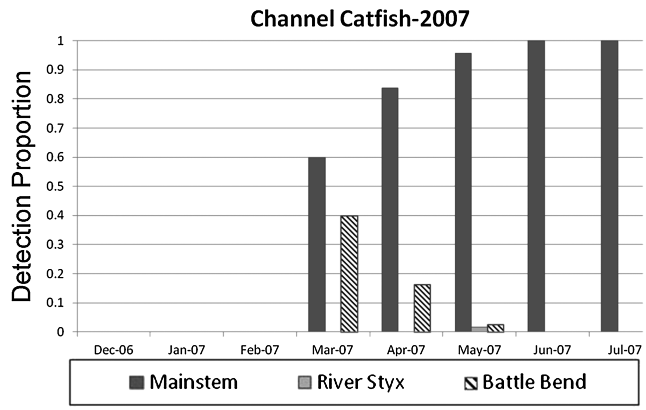

Figure 12. Proportion of detections of channel catfish during 2007 in the mainstem of the Apalachicola River (black bars), River Styx (grey bars) and Battle Bend (diagonal bars) as monthly proportions.

those years or by differences in the behaviour of the tagged subpopulations from each year; our study design did not allow for differentiation between these two effects. Relationships between initiation of spawning and water temperatures have been previously reported for many of these species (Mettee *et al*., 1996; Ross, 2001; Boschung and Mayden, 2004). Largemouth bass typically spawn when temperatures are between 14° and 24 °C, and in 2007, for example, this temperature range occurred between early March and early May (Figure 13) congruent with peak catches of *Micropterus* spp. larvae in light traps (Figure 11). Redear sunfish typically spawn when water temperatures are near 23 °C, and this temperature was first reached in early April 2007 (Figure 13) and matched with initial catches of larval *Lepomis* spp. for the year (Figure 4). Other larval specimens collected in light traps matched well with reported spawning temperatures.

In addition, aspects of the flow regime (timing, intensity and duration) are postulated to affect the timing of floodplain channel habitat use as well as spawn timing (Poff *et al*., 1997). Figure 13 shows plots of the discharge (m^3/s) in the Apalachicola River and indicates significantly lower flows during both of our study years compared to the 36-year mean discharge. Additionally, there were distinct differences in the flow patterns between 2006 and 2007. In 2006, there were more than five distinct pulses of increased flow lasting from March through July. In 2007, only two strong pulses occurred, one in early March and another in mid-April. The proportion of light traps catching larval spotted suckers in River Styx appeared to peak within one week following the second major discharge pulse during the spring for 2006 and 2007. *Micropterus* spp. movement to the floodplain and larval fish catches in light traps also appear to follow increases in flows in each year.

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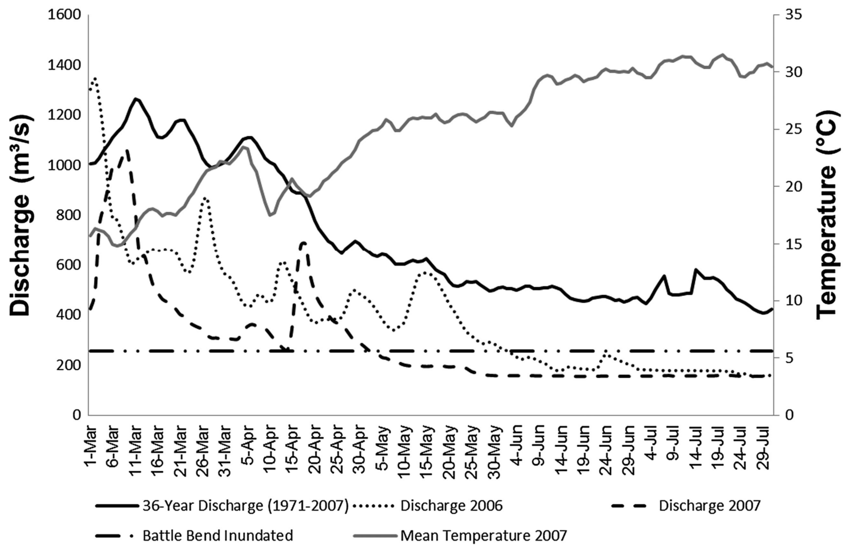

Figure 13. Plots of mean daily discharge (m^3/s) at Blountstown for 2006 and 2007 (dotted line; primary *y*-axis), 2007 (dashed line; primary *y*-axis), 36-year mean discharge (black line; primary y-axis) and water temperature (°C) (grey line; secondary *y*-axis) during spawning months (March–July). The intermittent dashed and dotted line represents the discharge level at which Battle Bend becomes inundated (approximately 255 m^3/s) as described by Light *et al*. (1998).

For all species in both years, there were representatives of individuals that remained in either the floodplain channel habitat only or mainstem habitat only (residents), as well as individuals that moved between the two habitat types (migratory individuals). Spotted sucker showed the most consistent behaviour between years, where at least 60% of individuals displayed migratory behaviour. Redear sunfish, largemouth bass and spotted bass all showed an increase in the per cent of individuals displaying migratory behaviour from 2006 to 2007, indicating that either environmental conditions differed in these years or that tagged individuals were representing behaviours of different subpopulations of the tagged species in each year. The mean individual ranges of species partitioned into resident and migratory behaviour categories emphasize the difference in behaviours of individuals within a species based upon habitat use patterns (Table II). Except for redear sunfish in 2007, all species in each year that used floodplain habitat only had smaller ranges than conspecifics that either used mainstem only or both habitats. This suggests that some individuals of each species are meeting their habitat requirements in either the floodplain channel or mainstem river habitats. Typically, species that are year-long residents of floodplain channel habitat are able to meet their day-to-day requirements throughout the year without expending the amount of energy required to meet their needs if they were migratory or year-long residents of the mainstem.

Home ranges for each species are difficult to compare with available literature because the number of studies that have reported home ranges for species in lotic environments is limited (Vokoun, 2003). Minns (1995) reviewed home range studies for fishes in lakes and rivers and reported home range values for largemouth bass from six studies of between 0.92 and 12.6 ha with mean reported values of 3.44 ha [Minns' values are reported in square metres (m^2) and converted to hectares for comparison]. This mean reported value is similar to home range estimates (95% UD; 2.87 ha) from this study for largemouth bass during 2006 (Table III). The 95% UD for largemouth bass in 2007 (33.08 ha) greatly exceeds any value reported in the comparison paper. Home range values reported by Minns (1995) for *Lepomis* spp. ranged from 0.0098 to 1.3 ha with a mean of reported values of 0.55 ha. All 95% UD calculations in this study for redear sunfish exceeded even the largest value reported for *Lepomis* spp. found in Minns (1995). There were no other tagged species in this study that were well represented by fishes in the comparison paper. The 50% UD calculations in this study were much closer to the values collected in the literature review by Minns (1995).

Minns (1995) notes important methodology differences in these studies that may explain differences in reported values. First, earlier lentic studies primarily used mark-recapture methods and calculated home ranges by using the average displacement as the radius of the home range. More recent lentic studies usually used telemetry methods for tracking movement and calculated home ranges using the minimum convex polygon. Additionally, for lotic studies, the primary method for detecting movement using mark-recapture and home ranges were calculated as the product of the average longitudinal displacement and the average stream width. There are pros and cons to each one of these methods. For instance, using the mark-recapture method for determining movement may work fine in lentic systems and lotic

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environments that are not morphologically complex. However, methods used to recapture tagged fish (netting, electrofishing and so on) are limited by sampling efforts and gear selectivity, so that many areas of a structurally complex study site may go unchecked, and thus, the movements of tagged individuals may not be accurately measured. It would not be feasible to attempt to recapture fish in all of the sloughs, tributaries, floodplains and in the mainstem of the Apalachicola River, although many species will use all of these habitats. In our study, the use of autonomous receivers greatly reduced the effort needed to collect movement data and produced results that are much more reliable compared with other potential methods.

Results herein also indicate that at least some proportion of the adults from each species studied used both habitats during a given year. With the exception of channel catfish (none were captured in light traps), there is also evidence that each of the species was using floodplain channel habitat as spawning grounds; thus, none of our study species are likely obligate floodplain spawners. There is also evidence that these same species will spawn in mainstem habitat, but in the case of *Micropterus* spp., *Lepomis* spp. and *M. melanops*, a greater proportion of larval catches occurred in the floodplain channel versus mainstem habitat. Although these species may have evolved to use floodplain habitat as spawning grounds and juveniles may use this habitat as rearing grounds, this study was not designed to determine if access to floodplain habitat is required for these species. Previous studies have linked floodplain inundation with increased yield of fishes in riverine systems (Bayley, 1991; Agostinho & Zalewski, 1995); however, methods used in our study did not allow for a quantitative assessment of such a linkage. In this study, we found that reconnection of historical portions of the Apalachicola River (Battle Bend) at a range of riverine flows provided backwater habitats that were used immediately by some species—an important result for natural resource managers of this system. Other species, such as spotted sucker, may not immediately utilize these backwater habitats for spawning grounds, possibly because of unsuitable habitat conditions. However, maintaining the connection and allowing for the natural interaction of floodplain habitats with the mainstem river may improve the conditions of these backwater habitats. In the future, species such as spotted sucker may find this habitat suitable as a spawning site.

CONCLUSIONS

Miranda (2005) presented a conceptual model for fish assemblages from oxbow lake systems in the lower Mississippi River valley that likely applies to the lower Apalachicola River. This model postulates that oxbow lake fish assemblages are structured by connectivity to the river and by abiotic factors that change over time as the interactions between the river and oxbow decline. The central concept in this model and others (Welcomme, 1995; Galat *et al*., 1998) is that flow events that connect floodplain and mainstem systems on regular (usually annual) intervals promotes connectivity between the floodplain and river, thus increasing the exchange of nutrients, sediments, lateral connectivity and fish between the two systems that directly affects community composition. When connectivity between these systems was lost, Miranda and Lucas (2004) and Miranda (2005) found that floodplain depth, surface area and shape changed and led to additional alterations to a suite of abiotic and biotic characteristics that directly and indirectly affected fish communities. Direct effects included loss of habitat via increased sedimentation that resulted in unsuitable spawning habitat for many fish species (e.g. Centrarchidae) and loss of woody structure that provided attachment sites for many macroinvertebrate species. As floodplain systems become more isolated, they often become shallower, leading to increased temperatures and susceptibility to hypoxic conditions during warm weather conditions, thus allowing for the dominance of species with higher tolerances for poor water quality. Disconnected floodplain systems often also have increased turbidity that reduces the foraging ability of many visual piscivores (e.g. *Micropterus* spp.) and often favours benthic feeders (e.g. *I. punctatus*).

A key concept in riverine ecology is that to maintain the ecological integrity of floodplain ecosystems, connectivity to the mainstem river environment is critical—to the point that this idea is considered an overarching theme in river restoration water management (Sparks, 1995). This idea was partially tested in this study through the restoration efforts to reconnect the Battle Bend floodplain to the mainstem Apalachicola River at a range of water levels. Our results provide some insight into this restoration effort as follows: (i) we documented the movement of adult fish from the mainstem Apalachicola River to the floodplain lake within weeks of completion of the construction project. Although passage by fish from the mainstem Apalachicola River to Battle Bend was possible during high water events in years prior to the restoration activities, our research shows that adult fish movement took place even during relatively lower flows in 2007; (ii) we documented a much lower proportion of light trap samples in the Battle Bend floodplain habitat with spotted sucker than in the River Styx floodplain. This may indicate that conditions are currently less suitable for spotted sucker spawning in Battle Bend than in River Styx. The spotted sucker is thought to spawn in areas associated with flowing water and, given hydrologic conditions during much of 2007, water flows in the Battle Bend floodplain were likely low; (iii) our telemetry results demonstrate, at the minimum, that a proportion of the adult *Micropterus*, *Lepomis* and *Minytrema* populations utilize only the mainstem or floodplain habitats and a proportion utilize both habitats during

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the spawning season. This is not surprising given the range of habitats available in both mainstem and backwater habitats and the generalized habitat use of the species studied, particularly the centrarchids (Carlander, 1977).

Overall, we found that *Micropterus* spp., *Lepomis* spp. and *M. melanops* used both mainstem and floodplain habitats during the spawning season and that some individuals of these species migrated to the floodplain prior to and concurrently with collections of larval fish of the same genus. These findings suggest that adult fish migrate to floodplain habitats, spawn in these habitats and that larval fish rear in these habitats, yet we are not able to provide evidence that access to floodplain habitats are required by populations of these fish species to remain viable. Separating habitat requirements from habitat use and selection will require further study, possibly on a landscape scale (Gunn and Sein, 2000).

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This paper is dedicated in memory of Rich Cailteux, scholar and friend, who researched fish populations in these river systems for many years. We would like to thank the University of Florida, Florida Fish and Wildlife Conservation Commission, US Geological Survey, and US Fish and Wildlife Service for their financial, logistical and administrative support. We are especially grateful to Charlie Mesing for his dedicated assistance during all phases of this study. Special thanks go to Joann Mossa and Tom Frazer whose early revisions improved this manuscript. We would also like to thank Elissa Buttermore, Ed Camp, Kevin Johnson, Drew Dutterer, Jared Flowers, Colin Hutton, Matt Lauretta, Lauren Marcinkiewicz, Darren Pecora and Jake Tetzlaff for their help in collecting data and analysing samples. The authors have no conflicts of interest related to the publication of this manuscript.

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APPENDIX: NUMBER OF FISH TAGGED AND NUMBERS USED TO MAKE CALCULATIONS.

A. Year 2006

Species	Number tagged	Tag manufacturer	Number never detected	Number used to calculate habitat use	Number used to determine movement category	Number used to calculate LCP home range	Number used to calculate ArcView home range
Lepomis microlophus	20	10 Vemco/10 ATS	0	6	5	1	0
Micropterus salmoides	22	11 Vemco/11 ATS	0	11	9	3	2
Micropterus punctulatus	18	9 Vemco/9 ATS	0	9	7	6	5
Minytrema melanops	20	9 Vemco/11 ATS	0	8	8	2	2
Ictalurus punctatus	0	—	0	0	0	0	0

B. Year 2007

Species	Number tagged	Tag manufacturer	Number never detected	Number used to calculate habitat use	Number used to determine movement category	Number used to calculate LCP home range	Number used to calculate ArcView home range
Lepomis microlophus	30	30 Vemco	0	23	20	7	6
Micropterus salmoides	24	24 Vemco	0	23	21	14	8
Micropterus punctulatus	6	6 Vemco	0	5	5	2	2
Minytrema melanops	30	30 Vemco	0	25	25	14	9
Ictalurus punctatus	30	30 Vemco	0	24	20	7	9

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