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Swimways: Protecting Paddlefish through Movement-centered Management

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Abstract
Attempts to mitigate lack of formal interjurisdictional paddlefish management have been made in the United States through the Mississippi River Interstate Cooperative Resource Association (MICRA). We used 1988–2009 data from the MICRA paddlefish (*Polyodon spathula*) stock assessment database—a database containing mark–recapture and biometric information on more than 30,000 individually marked wild paddlefish and more than 2 million hatchery-origin paddlefish—to estimate survival and movement across large and potentially biologically relevant spatial scales. Paddlefish frequently moved between political jurisdictions with differing conservation strategies and harvest regulations and showed differences in survival parameter estimates throughout their range. We argue that the degree of interjursidictional movements, spatially variant survival rates, and conservation concerns associated with paddlefish necessitate more cohesive interjurisdictional management. Based on criteria used to establish flyways for migratory bird management, we offer swimways as a potential spatial configuration for biologically relevant management units.

Corredores de nado: protección del pez espátula mediante manejo centrado en su movimiento

Resumen: La Asociación Interestatal de Recursos Cooperativos del Río Mississippi (AIRCRM) ha hecho intentos para mitigar la falta de manejo inter-jurisdiccional del pez espátula en los EEUU. Se utilizó información sobre evaluación de los stocks de pez espátula (*Polyodon spathula*) contenida en la base de datos de AIRCRM para el periodo 1995-2009, la cual contiene información biométrica y de marca-recaptura de >30,000 peces espátula marcados individualmente y de >2 milliones de especímenes provenientes de cultivo, con el fin de estimar la supervivencia y movimiento a escalas espaciales amplias y con potencial biológico relevante. El pez espátula frecuentemente se mueve entre jurisdicciones políticas que difieren en cuanto a sus estrategias de conservación y regulaciones de captura, y muestra diferencias en sus parámetros de supervivencia a lo largo de su ámbito geográfico. Se argumenta que el grado de movimiento inter-jurisdiccional, el cambio espacial en las tasas de supervivencia y las preocupaciones de conservación asociadas a esta especie, demandan de un manejo inter-jurisdiccional con mayor cohesión. Sobre la base de criterios usados para establecer corredores de vuelo para el manejo de aves migratorias, aquí se muestra un corredor de nado como una potencial configuración espacial para unidades de manejo biológicamente-relevantes.

Introduction

Habitat alteration, overexploitation, and climate change have led to declines in terrestrial and aquatic migratory animals at a global scale (Dudgeon et al. 2006; Wilcove and Wikelski 2008). Mitigating biodiversity losses of migratory species poses challenges for conservation scientists and managers because migrations often exist at spatial scales exceeding that of data collection programs and jurisdictions of management entities. The result of data-scale limitations is a potentially incorrect understanding of population trajectories due to a limited understanding of the contribution of migratory movements to life histories or population dynamics (Wilcove and Wikelski 2008). Effective conservation for migratory animals will thus require increased knowledge of migratory movements at biologically relevant spatial scales to protect biota from current and future threats (Wilcove and Wikelski 2008).

Global declines of freshwater migratory fishes have been paralleled by the American paddlefish (*Polyodon spathula*), which has experienced declines as a result of habitat loss, blocked migrations, and alteration of natural flow regimes (Jennings and Zigler 2009). Paddlefish are also a highly valued commercial fish due to their popular caviar and thus have faced growing threats from overharvest as global sturgeon stocks have collapsed. However, consensus on how to most effectively manage this species in a way that offsets threats has not been reached due in part to a near complete absence of basic knowledge about the frequency, scale, or life history significance of their long-distance movements.

Perhaps more important, consensus on how to best manage paddlefish to protect them from threats has not occurred because fisheries management of inland waters of

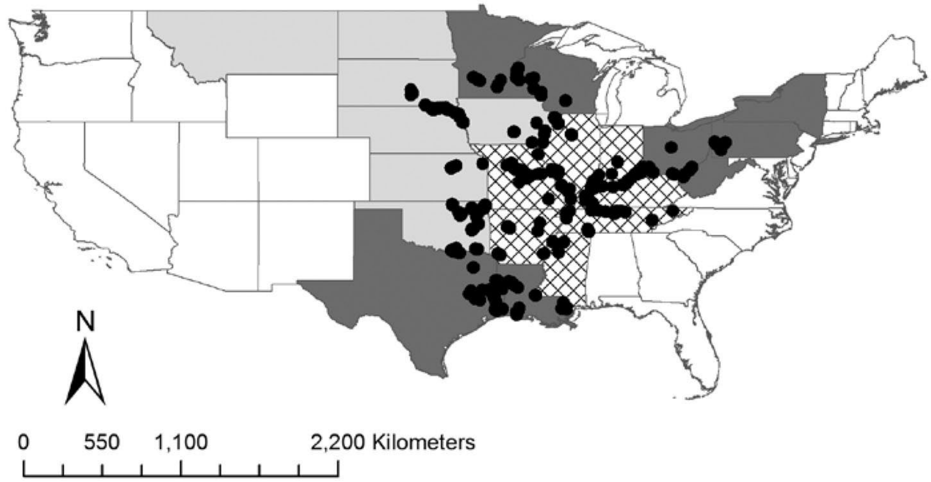

Figure 1. Map of collection sites as included in the Mississippi Interstate Cooperative Resource Association paddlefish stock assessment database from 1995 to 2009 (black dots). Type of harvest allowed in each state is indicated by shading: no harvest (dark gray); sport harvest (light gray); sport and commercial harvest (cross-hatch). Harvest status obtained from Bettoli et al. (2009).

the United States, even that of migratory fishes reported to make interjurisdictional movements, is accomplished on a state-by-state basis. For instance, one marked paddlefish was reported to move in excess of 1,600 river kilometers (rkm) from South Dakota to Kentucky (Stancill et al. 2002). This paddlefish moved through no less than seven management jurisdictions, each with different conservation objectives and harvest regulations during its 1,600-rkm movement. Moreover, because paddlefish are able to traverse political boundaries, management decisions from one state may impact management outcomes unpredictably in other states because there is currently no understanding of interactions between interjurisdictional movements and population dynamics.

Some attempts have been made to implement interjurisdictional paddlefish conservation and management measures through voluntary state agreements that any state can opt out of at any point. The Mississippi River Interstate Cooperative Resource Association (MICRA) is one such cooperative entity seeking to provide coordinated sampling, management, and conservation of acipenserid fishes of the Mississippi River Basin among its member states through its Paddlefish and Sturgeon Committee. The MICRA relies on voluntary cooperation among member states from within the basin, the United States Fish and Wildlife Service, Tennessee Valley Authority, U.S. Bureau of Reclamation, U.S. Geological Survey, Chickasaw Indian Nation, and the Chippewa-Cree Indian Tribe. The MICRA Paddlefish and Sturgeon Committee began a voluntary, basin-wide paddlefish stock assessment in 1995 consisting of a nearly species range-wide, mark–recapture study. Data from this massive state-funded sampling effort has been deposited in a centralized database (hereafter, MICRA database) that also contains hatchery release and recapture information since 1988. We used the MICRA database to provide the first-ever description of basic vital rates (i.e., survival and movement) for paddlefish—or for any freshwater migratory fish—at this scale. We also used this database to gain a better understanding of the extent and frequency of interjurisdictional paddlefish movements. Our specific objectives were to (1) describe intrajurisdictional and interjurisdictional movements of wild and stocked paddlefish at a nearly species extent scale; (2) quantify survival (S), movement (ψ), and recapture (ρ) probabilities across major river basins (e.g., Missouri, Mississippi, Ohio, Gulf) for wild and stocked paddlefish; and (3) use large-scale biological data to provide an example of how movement-based management units for paddlefish could be constructed.

Materials and Methods

Data Set

The MICRA paddlefish stock assessment project encompasses the 22 states that represent the current distribution of paddlefish. Within this area, harvest regulations and conservation status of paddlefish vary and range from being a protected species to one that is harvested both recreationally and commercially (Figure 1). The MICRA database is a compilation of data collected by cooperating states from 1995 to present and contains morphometric information such as length and weight, as well as habitat information such as flow velocity and water quality where paddlefish were captured. This database additionally contains information from 1988 to the present on dates and stocking locations of all hatchery-reared, stocked paddlefish from the MICRA project area. All encountered paddlefish (hatchery- and wild-origin) were marked with an individually numbered coded wire tag (CWT; Northwest Marine Technologies, Shaw Island, WA) inserted in their rostrum at the time of capture from 1995 through 2006. Coded wire tags were located with a CWT detecting wand (Northwest Marine Technologies), cut out of the rostrum and replaced with a new individually numbered CWT upon recapture. Coded wire tags were removed from the rostrum because the tag can only be decoded by reading a series of physical marks on the tag under a microscope. The years 2007 through 2009 were treated as a recapture-only period, where no new fish entered into the study because the use of CWTs for wild fish was discontinued by MICRA, although stocked paddlefish continue to be marked with CWTs to the present. The CWTs were replaced with individually numbered metal jaw tags during the recapture-only period to differentiate previously marked from unmarked paddlefish. More than 40 differ-

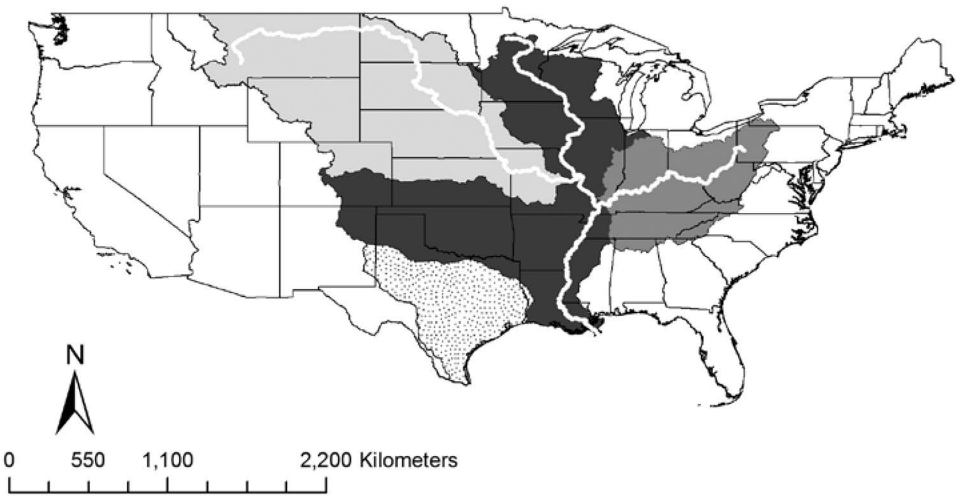

Figure 2. River basin designation as listed in the Mississippi Interstate Cooperative Resource Association paddlefish stock assessment database. River basins are designated as follows: light gray, Missouri Basin; dark gray, Mississippi Basin; medium gray, Ohio Basin; stipple, Gulf Basin.

ent gear types were used by biologists over the course of the MICRA study period; thus, standard effort calculations by gear type were cumbersome. We quantified hours of biologist sampling effort by basin by summing the hours of sampling effort across all gear types. We used the number of CWT recaptures from commercial and sport harvest as a proxy for harvest effort because the MICRA database does not contain harvest effort information. Unknown numbers of unreported CWTed paddlefish are recaptured by sport and commercial anglers. Coded wire tags are inconspicuous and cannot be detected without a CWT detector wand; thus, anglers do not know when they have recaptured a CWTed paddlefish. Discussion of recaptured paddlefish refers only to reported recaptures and we acknowledge that the actual numbers of recaptures are likely higher than those reported in the MICRA database.

Data Analysis

We quantified intrajurisdictional (within a state) and interjurisdictional (between states) movements of paddlefish at multiple spatial scales by enumerating movements of wild and stocked paddlefish from one state to another. The large number of sampling gears used to collect fish in the MICRA database prohibited many standard fishery population analyses that require gear-specific catches to account for size selective gear bias. Therefore, we used multistate mark–recapture (MSMR) analyses (Hestbeck et al. 1991; Brownie et al. 1993) in Program MARK (multistate recaptures only model; White and Burnham 1999) to compute maximum-likelihood estimates of survival (S), recapture (ρ), and movement (ψ) probabilities. A benefit of this approach is that ρ can account for unequal effort (Steffensen et al. 2010), allowing us to capitalize on the large spatial and temporal scale of data in this database despite the lack of gear consistency.

We determined whether individual paddlefish were of hatchery- or wild-origin from tagging information found within the database and then assigned those origins to each fish for initial capture and all recaptures throughout its life. States are the current management unit for migratory fishes; however, the data in the MICRA database were too sparse to allow for informative state-specific analyses of S, ρ, and ψ. Instead, we pooled states within river basins to estimate S, ρ, and ψ. We used river basins as designated in the MICRA database (Figure 2): Gulf Basin (*G*: rivers that drain directly into the Gulf of Mexico), Missouri Basin (*Mo*: Missouri River and its tributaries), Mississippi Basin (*Ms*: Mississippi River and its tributaries, excluding the Missouri and Ohio rivers), and Ohio Basin (*O*: Ohio River and its tributaries). We conducted MSMR analyses using only wild-origin paddlefish collected from 1995 to 2009 (the duration of the MICRA project) to provide estimates of population vital rates (S, ρ, and ψ) at the scale of river basins. Like the state-level mark–recapture data, mark–recapture data for hatchery-origin paddlefish from 1988 to 2009 were also too sparse to yield parameter estimates and were not included.

We considered three competing models to evaluate hypotheses regarding temporal variation in survival and movement estimates. Capture and recapture periods were designated as a calendar year running from January 1 to December 31. All models included basin-specific (indicated by subscript B) estimates. Our models included a null model with time constant S and ψ (S_B, ρ_B, *and* ψ_B). Four more complex models were considered: time- and basin-specific S(S_{B*t}, ρ_B, *and* ψ_B); time- and basin-specific ρ(S_B, ρ_{B*t}, and ψ_B); time- and basin-specific ψ(S_B, ρ_B, and ψ_{B*t}); and time- and basin-specific S, ρ, and ψ(S_{B*t}, ρ_{B*t}, and ψ_{B*t}). Each basin-specific estimate of S, ρ, and/or ψ and/or time-specific estimate of S and/or ψ represented one parameter in the estimation models. Estimates of basin-specific rates of emigration, ψ, resulted in estimates of ψ_{rs}, the annual probability of moving from a basin of origin, r, to all potential destinations, s (e.g., with the Gulf as the source basin: ψ_{GO}, ψ_{GMo}, ψ_{GMs}). The annual probability of not emigrating, ψ_{rr}, can be estimated as the complement of the sum of all ψ_{rs} (e.g., $\psi_{GG} = 1 - [\psi_{GO} - \psi_{GMo} - \psi_{GMs}]$; Brownie et al. 1993). The probability of not emigrating from a basin over a period of years (y) is calculated as: ψ_{rry}.

Movement parameters, ψ_{rs} (e.g., ψ_{MoMs}: Missouri Basin to Mississippi Basin; ψ_{OMs}: Ohio Basin to Mississippi Basin; etc.), were fixed to zero when movement between basins was not recorded in the MICRA database. Movement parameters that were fixed to zero in the MSMR analysis included the Gulf Basin to all basins and the Missouri Basin to the Ohio Basin (although not the reciprocal). There was one movement from the Ohio Basin to the Missouri Basin in the MICRA database, but we were unable to include this in the MSMR analysis because it was not associated with a recapture year. However, we did include this movement in state-specific movement tallies. We selected the best model among the three considered with Akaike's information criterion (AIC); the model with the lowest AIC was considered the best model, and model weights were used to assess the strength of the top model, relative to the other models. We used 95% confidence intervals to compare parameter estimates between river basins.

Results

Data Analysis

A total of 22,231 wild paddlefish was marked from 1995 to 2006 (Table 1). Biologist and sport harvest accounted for the most common source of recaptures in the MICRA database, with commercial harvest accounting for less than 10% of all recaptures (Table 2). The Ohio Basin had the largest amount of biologist effort (Figure 3) and issued the most marks, although the largest number of recaptures occurred in the Missouri Basin (Table 1). Most movements of wild paddlefish (as determined by state of initial capture and state of recapture) occurred within a single state (61%; 1,011 of 1,655; Table 3). However, 39% of movements of wild paddlefish occurred across state boundaries (644 of 1,655) with movements out of river basins accounting for 2% of interjurisdictional movements (14 of 644) and 1% of total movements (14 of 1,655).

A total of 2,535,787 marked paddlefish was stocked from 1988 to 2009 (Table 1). Similar to wild paddlefish, most movements of hatchery-origin paddlefish occurred within the state that originated the stocking (71%; 1,616 of 2,261; Table 4). Interjurisdictional movements did take place: 29% of recaptures indicated movements outside the state of original stocking (645 of 2,261), with movements out of river basins accounting for less than 1% of interjurisdictional movements (1 of 645). Most interjurisdictional movements of hatchery-origin paddlefish originated from two states: Kansas, where 93% (183 of 196) of recaptures indicated movement outside of Kansas, and South Dakota, where 36% (448 of 1,244) of recaptures indicated movement outside of South Dakota.

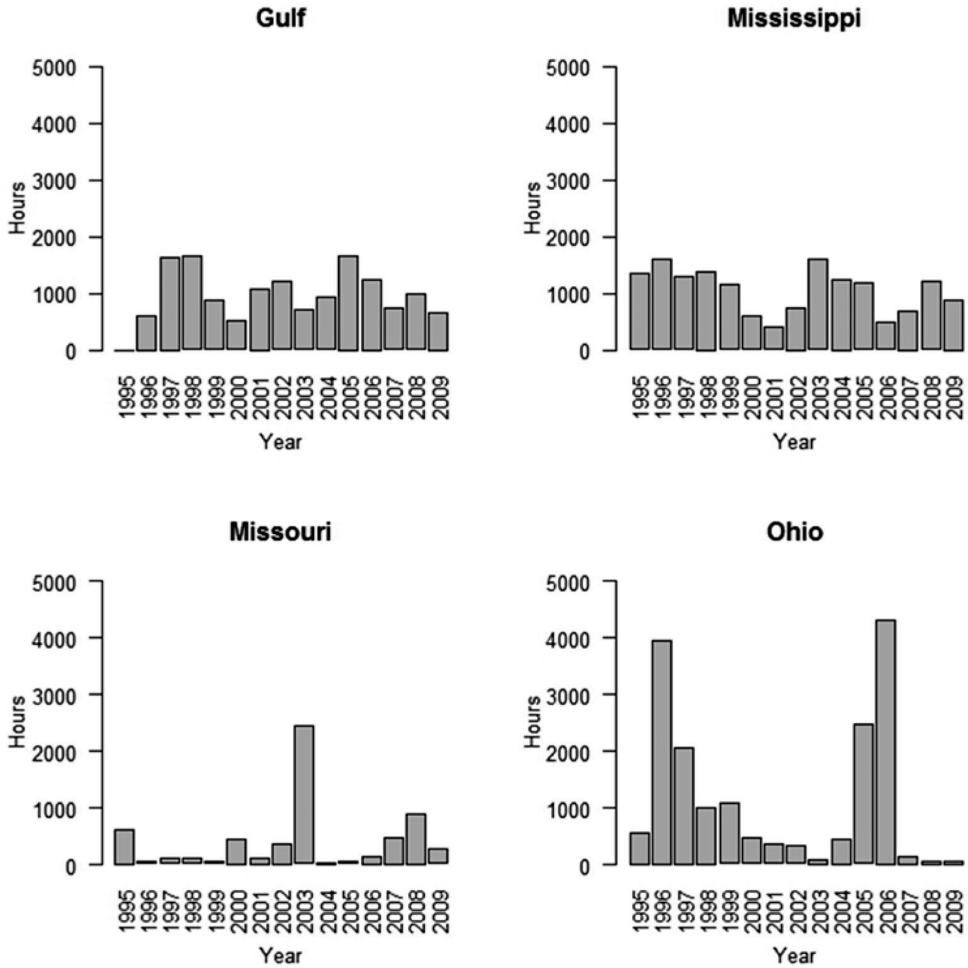

Figure 3. Biologist sampling effort (hours of effort) by year summed across all gear types for each river basin in the Mississippi Interstate Cooperative Resource Association paddlefish stock assessment database from 1995 to 2009

Table 1. Numbers of wild- and hatchery-origin paddlefish marked and recaptured in the MICRA paddlefish stock assessment study.

	Gulf	Mississippi	Missouri	Ohio
Wild Marked	701	6,111	6,797	8,622
Recaptured	29	565	1,759	933
Hatchery Marked	1,059,375	262,270	1,092,724	121,418
Recaptured	339	582	1,797	29

The simplest (time constant) model (S_B, ρ_B, and ψ_B) for wild paddlefish had a lower AIC value than the two time-specific models, and we selected it as the best model because it received 100% of the model weight (Table 5). The models including ρ_{B*t} did not converge, thus we could not evaluate models with time-specific ρ among others in model selection. The best basin-level estimates of S, ρ, and ψ were not time specific, so the information obtained from the MICRA database should be inter-basin during the study period. Estimates of S, ρ, and ψ differed among basins (Table 6). The Missouri Basin had the highest S and ρ, the Mississippi River Basin had the lowest S, and the Gulf Basin had the lowest ρ (Table 6). Estimates from the Gulf Basin could not be distinguished from other basins (Table 6). Furthermore, there was no movement recorded to or from the Gulf Basin, likely due to the absence of fresh-

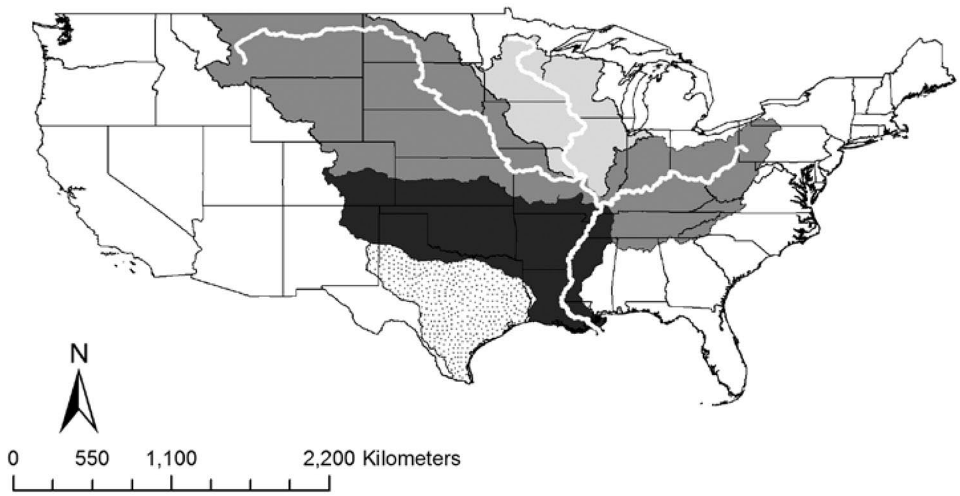

Figure 4. Potential swimway management framework constructed using paddlefish movements recorded in the 1995 to 2009 Mississippi Interstate Cooperative Resource Association paddlefish stock assessment database. Management units are designated as follows: medium gray, Missouri–Middle Mississippi–Ohio management unit; light gray, Upper Mississippi management unit; dark gray, Lower Mississippi management unit; stipple, Gulf management unit.

water connections with other basins; therefore, Gulf Basin parameter estimates will not be discussed further. Wild paddlefish movements on an annual scale appear to be generally confined within a river basin as shown by low ψ probabilities (Table 6), a notion that is further supported by tallies of movements of wild paddlefish (Table 3). Interbasin movements were most common from the Missouri to Mississippi basin and the reciprocal and from the Mississippi to the Ohio basin but not the reciprocal (Table 6). However, although interbasin ψ on an annual scale was low, extrapolating ψ probabilities over time shows that over periods of 10, 20, and 30 years—time periods biologically relevant to paddlefish that can have life spans longer than 50 years—probabilities of emigrating from a basin increase to as much as 0.27 over 30 years (Table 7).

We used interbasin paddlefish movement information from Tables 3–7 to construct swimways: potential spatial management units for paddlefish (Figure 4). Interbasin movements of paddlefish were largely restricted to the Missouri–Mississippi– Ohio basins. We connected the Missouri and Ohio river basins through the Middle Mississippi River (Mississippi River from the confluence of the Missouri and Mississippi rivers to the confluence of the Ohio and Mississippi rivers) as a swimway management unit. Movement between the Lower Mississippi River (below the confluence of the Ohio and Mississippi rivers) and other river basins or between the Upper Mississippi River (above the confluence of the Missouri and Mississippi rivers) and other river basins was not recorded, and these river basins were delineated as separate swimway management units as a result. However, the lack of recorded interbasin movements from paddlefish tagged in the Upper Mississippi River or the Lower Mississippi River may be due to a relatively low number of marked and recaptured paddlefish and not necessarily due to a lack of movement.

Table 2. Percentages of coded wire tagged paddlefish recaptured by biologists, commercial anglers, sport anglers, and other (i.e., found dead, unknown) methods in each subbasin in the MICRA paddlefish stock assessment study

	Gulf	Mississippi	Missouri	Ohio
Biologist	99	55	35	52
Commercial	0	11	0	44
Sport	0	34	64	<1
Other	1	<1	1	4

Discussion

Interjurisdictional management of paddlefish is currently the exception rather than the rule even though paddlefish frequently traverse management boundaries (i.e., state boundaries). To some degree, this lack of interjurisdictional management has been a consequence of a near complete absence of basic, large-scale data on these fish that could inform biologically relevant management boundaries. This study provides the first description of large-scale movements of not only paddlefish but of any potadromous fish that could be used to create larger, biologically informed management boundaries. In comparison, migratory waterfowl flyways—movement corridors of migratory waterfowl that serve as management boundaries—were established in 1948 based on long-term mark–recapture studies documenting migratory pathways (Boere and Stroud 2006). These movement corridors are the foundation for the administration of harvest regulations and establishment of research and management priorities for migratory waterfowl. Based on the movement data compiled by the MICRA database and the flyway management framework used for migratory waterfowl, we offer a potential swimway management framework for paddlefish (Figure 4). The swimway management unit configuration we offer joins river basins where our analyses show that interbasin paddlefish movement occurs, translating paddlefish mark–recapture information into a potential spatial management framework. Interjurisdictional swimway management for paddlefish of the greater Mississippi River Basin could be administered in a similar fashion to migratory waterfowl flyways where representatives from Canadian provinces and U.S. and Mexican states partake in flyway councils to set broad restrictions for local governing bodies (Boere and Stroud 2006). The flyway management framework allows local governing bodies to be more, but not less, restrictive than the guidelines set forth by the flyway council. Swimway manage-

Table 3. Total number of movements and number of coded-wire tagged (CWT) wild-origin paddlefish obtained from the MICRA database by state postal abbreviation. Intrastate movements (marked and recaptured in the same state) are listed on the diagonal with the top number indicating the number of recaptures and the bottom number indicating the total number of paddlefish CWT by a state. Interstate movements (marked in one state and recaptured in a different state) are listed on the off-diagonal where fish were tagged in the state listed in the row and recaptured in the state listed in the column. Light-gray, outlined boxes indicate movement between adjacent states within a basin; medium-gray boxes indicate movement between nonadjacent states within a basin; and black boxes indicate movement between basins.

	AR	IL*	IN*	IA†	KS†	KY*	LA†	MN‡	MS*	MO*	NE†	OH‡	OK†	PA‡	SD†	TN*	TX‡	WV‡	WI‡
AR	4 31																		
IL*		190 5,446	6			28				3	3				3	1			
IN*		10	130 2,415			30						10			1				
IA†				138 2,938							2				8				
KS†					0 63														
KY*		6	37			59 2,578						1			1				
LA†							14 682												
MN‡				1				0 35											
MS*						1			0 120										
MO*						1				6 242									
NE†				4						3	172 3,513				339				
OH‡			11			7						39 489							
OK†													0 74						
PA‡														2 3					
SD†		3		3		1				4	110				247 2,717				
TN*						1				1						9 406			
TX‡																	1 29		
WV‡						1						1						0 55	
WI‡				2															0 395

+ State allowing commercial and sport paddlefish harvest.
† State allowing paddlefish sport harvest.
‡ State with paddlefish harvest prohibited.

ment could be administered in a similar fashion where swimway councils could be assembled to create sets of minimum restrictions that would allow local management entities to be more, but not less, restrictive than the restrictions set forth by the swimway council.

Although transitioning to a larger, interjurisdictional management framework for paddlefish would require a paradigm shift in riverine fisheries management in the United States, our study provides substantial evidence as to why a larger management framework is necessary. Perhaps the most compelling evidence for the need for interjurisdictional management comes from the frequency of movements across jurisdictional boundaries. Management actions conducted by a jurisdiction, such as harvest regulations or stocking plans, are meant to influence populations and, given the high mobility of paddlefish, multiple management jurisdictions can influence populations simultaneously. Large rivers frequently serve as state boundaries, creating border waters that are managed by multiple management jurisdictions. Although some states cooperatively manage border waters (Argent et al. 2009; Mestl and Sorensen 2009), cooperative management frameworks are usually voluntary and can be voided unilaterally by individual states. Movements between bordering states are the most common type of interjurisdictional movement and areas where rivers form jurisdictional borders are where paddlefish populations have the greatest potential of being affected by management disconnects. Ohio and Kentucky, for instance, share the Ohio River as a border. Ohio lists the paddlefish as a state threatened species, whereas Kentucky allows harvest (both commercial and sport). In this case, fishing regulations governing angler take are determined by the side of the river where harvest is occurring: anglers on the Ohio side of the river are prohibited from fishing for paddlefish, whereas anglers on the Kentucky side of the river are allowed to harvest paddlefish with the appropriate permits. It would be naïve to think that in this instance the Ohio paddlefish population is somehow distinct from the Kentucky paddlefish population, particularly due to the high frequency of movements between these two states. Although such dramatic management disconnects as exist between Ohio and Kentucky are currently unique to these states, there is no larger management framework preventing proliferation of such mutually exclusive management objectives in other bordering states in the greater Mississippi River Basin. Moreover, effects of the dramatic management disconnects among states across the species range can be seen at a larger spatial scale. For example, the two basins allowing commercial harvest (i.e., Mississippi and Ohio) had the lowest survival probabilities (Table 3) and the highest probabilities of emigration. Taken

Table 4. Total number of movements of coded-wire tagged (CWT) hatchery-origin paddlefish obtained from the MICRA database by state postal abbreviation. Intrastate movements (stocked and recaptured in the same state) are listed on the diagonal with the top number indicating the number of recaptures and the bottom number indicating the total number of CWT paddlefish stocked by a state. Interstate movements (stocked in one state and recaptured in a different state) are listed on the off-diagonal where the state of capture is listed in rows and the state of recapture is listed in the columns. Recaptures indicating movement of a stocked paddlefish from a state that does not stock paddlefish back into the state that originally conducted the stocking is considered an intrastate movement in this tally. Light-gray, outlined boxes indicate movement between adjacent states within a basin; medium-gray boxes indicate movement between nonadjacent states within a basin; and black boxes indicate movement between basins.

	AR*	IN*	IA†	KS†	KY*	LA†	MO*	ND†	NE†	NY‡	OH‡	OK†	PA‡	SD†	TN*	TX‡	WV‡
AR*	16 17,388																
IN*		0 0															
IA†			0 0														
KS†			1	13 47,405			1		66			13		102			
KY*		1			0 1,800												
LA†						7 186,866											
MO*					1		450 739,580		1					5			
ND†								0 19,037									
NE†									0 0								
NY‡										2 8,621			1				
OH‡											0 0						
OK†												314 203,434					
PA‡					1								2 76,341				
SD†			2	1			1		444					796 424,136			
TN*					1										5 12,982		
TX‡																6 771,135	
WV‡											2		1				5 27,062

+ State allowing commercial and sport paddlefish harvest.
† State allowing paddlefish sport harvest.
‡ State with paddlefish harvest prohibited.

Table 5. Competing models for survival (S), recapture (ρ), and movement (ψ) probabilities of wild paddlefish across their range in the greater Mississippi River Basin of the United States from 1995 to 2009 ranked by Akaike's information criteria (AIC), where k is the number of parameters, ΔAIC is the difference between AIC values from each model, and WAIC is the Akaike weight (all weights sum to 1).

Model[a]	k	AIC	ΔAIC	WAIC
S_B, ρ_B, ψ_B	12	17,231.53	0.00	1.00
S_{B*t}, ρ_B, ψ_B	20	17,249.06	17.53	0.00
S_B, ρ_B, ψ_{B*t}	26	17,504.91	273.38	0.00

a. Survival as time- and basin-specific (S_{B*t}) or time constant (S_B), recapture probability as time constant and basin-specific (ρ_B), and movement as time- and basin-specific (ψ_{B*t}) or time constant (ψ_B).

together, the combination of mortality and emigration evident in the Mississippi River Basin should result in fewer fish. Conversely, states located in the Missouri Basin—the subbasin where no state allows commercial harvest—had the highest survival probability. These differences in survival among basins are influenced by commercial harvest, indicating that state management actions may scale-up to effects at the basin level, further supporting the need for a larger management framework.

Stocking hatchery-origin paddlefish is widespread throughout the greater Mississippi River Basin, and low numbers of recaptures relative to the number of fish stocked leaves us unable to quantify basic vital rates of these fish to the overall population. However, we do know from this study and previous studies that hatchery fish frequently move outside of the jurisdiction that originally conducted the stocking (Pracheil 2010; Pierce et al. 2011). Hatchery rearing of fish has been implicated in individual effects such as reduced fecundity (Chilcote 2003), reduced genetic diversity (Sloss et al. 2009), reduced fitness in the wild, and lower survival when compared to their wild-produced counterparts (Howell 1994) that may upscale to population-level effects including genetic introgression of the wild population (Araki and Schmid 2010). Paddlefish are not exempt from genetic effects of stocking, and reduced genetic diversity has been reported from hatchery-reared paddlefish (Sloss et al. 2009). Moreover, paddlefish are long-lived (>40 years; Scarnecchia et al. 2006; Pracheil 2010), creating the potential for long-lasting population effects if genetic differences between hatchery- and wild-origin individuals have phenotypic expressions. These reasons and others, such as state-by-state variability in management objectives (e.g., stocking for conservation, stocking to supplement sport harvest), stocking strategies (e.g., no stocking, stocking large numbers of fingerlings), and broodstock selection techniques (i.e., selecting the first several fish collected that meet maturation criteria, selecting broodstock based on genetic

Table 6. Survival (S_B), recapture (ρ_B), and movement (ψ_{rs}) probabilities (95% confidence estimates) by river basin (*B*) for wild paddlefish in the Mississippi Interstate Cooperative Resource Association Paddlefish Stock Assessment Database from 1995 to 2009 where basins listed in rows are originating basin of movement (*r*) and basins listed in columns are basins receiving fish (*s*).

	Receiving Basin			
Origin basin	Gulf (*G*)	Missouri (*Mo*)	Mississippi (*Ms*)	Ohio (*O*)
Gulf	S_G = 0.7818[a] (0.5498–0.9132) ρ_G = 0.0018a (0.0007–0.0047) Ψ_{GG} = 1.0000	Ψ_{GMo} = 0b	Ψ_{GMs} = 0	Ψ_{GO} = 0
Missouri	Ψ_{MoG} = 0	S_{Mo} = 0.8591 (0.8416–0.8750) P_{Mo} = 0.0288 (0.0260–0.0318) Ψ_{MoMo} = 0.9987	Ψ_{MoMs} = 0.0013 (0.0002–0.0092)	Ψ_{MoO} = 0
Mississippi	Ψ_{MsG} = 0	Ψ_{MsMo} = 0.0033 (0.0016–0.0072)	S_{Ms} = 0.6448 (0.5890–0.6969) ρ_{Ms} = 0.0095 (0.0074–0.0121) Ψ_{MsMs} = 0.9897	Ψ_{MsO} = 0.0070 (0.0028–0.0171)
Ohio	Ψ_{OG} = 0	Ψ_{OMo} = 0.0006 (0.0002–0.0026)	Ψ_{OMs} = <0.0001c	S_O = 0.7885 (0.7522–0.8207) ρ_O = 0.0113 (0.0094–0.0136) Ψ_{OO} = 0.9994

a. S_B and ρ_B estimates are given on the diagonal.
b. Ψ_{rs} estimates between basins are given on the off-diagonal.
c. 95% confidence interval included.

criteria; Grady and Elkington 2009), suggest that a larger management framework is needed.

Conclusions

Gathering data at a range-wide scale is exceptionally difficult, particularly due to the autonomous nature of fisheries management in the greater Mississippi River Basin and the voluntary participation of individual states in cooperative management and data collection agreements. The MICRA paddlefish stock assessment effort is therefore an unprecedented, improbable, and heroic effort that has been voluntarily coordinated, funded, and conducted by individual states since the 1990s. Unfortunately, the MICRA paddlefish stock assessment effort has recently been downscaled, jeopardizing this globally unique resource among all potadromous fishes that can be used to inform fisheries management in the face of growing population threats and high future uncertainty. Creating an interjurisdictional management framework using swimway councils to set research and management priorities may be one way to protect this data resource and to create management jurisdictions with biological relevancy.

Threats facing paddlefish are similar to those encountered by managers in other large-scale management scenarios (e.g., migratory birds) that require explicit cooperation among state, federal, and other stakeholders. Creating a movement-based management framework centered on known population connections may be one way to buffer species against these threats. Though we did not focus on the effects of dams on paddlefish population fragmentation in this study, paddlefish movement through dams is common (Brown 1951; Zigler et al. 2003; Pracheil 2010), with literature reports of movement through up to five dams (Stancill et al. 2002). The spatial framework we offer cannot totally ameliorate the effects of population fragmentation caused by large dams that totally or partially block upstream movement. However, the swimway framework would facilitate common management in areas where populations appear connected by movement. Moreover, restoration of large river ecosystems that removes alterations such as dams and channelization at the source of population declines is oftentimes not possible due to the human reliance on the ecosystem services of the altered river. Creating a proactive, interjurisdictional management plan that capitalizes on known population connections may be one of the few mechanisms we have to protect paddlefish stocks from further declines.

Table 7. Ten-, 20-, and 30-year estimates of the probability of not emigrating (ψ_{rr}) from a river basin (*r*) for wild paddlefish in the Mississippi Interstate Cooperative Resource Association Paddlefish Stock Assessment Database from 1995 to 2009. Basins used in analyses include Gulf (*G*), Missouri (*Mo*), Mississippi (*Ms*), and Ohio (*O*). Period transition rates are calculated as exponential functions of annual rates of not emigrating from Table 4.

Parameter	Annual	10-Year	20-Year	30-Year
Ψ_{GG}	1.0000	1.00	1.00	1.00
Ψ_{MoMo}	0.9987	0.98	0.97	0.96
Ψ_{MsMs}	0.9897	0.90	0.81	0.73
Ψ_{OO}	0.9994	0.99	0.99	0.98

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References

Araki, H., and C. Schmid. 2010. Is hatchery stocking a help or harm?: Evidence, limitations and future directions in ecological and genetic surveys. *Aquaculture* 208:S2–S11.

Argent, D. G., W. G. Kimmel, R. Lorson, P. McKeown, D. M. Carlson, and M. Clancy. 2009. Paddlefish restoration to the Upper Ohio and Allegheny river systems. Pages 397–410 in C. P. Paukert and G. D. Scholten, eds. *Paddlefish management, propagation, and conservation in the 21st century: Building from 20 years of research and management.* American Fisheries Society, Symposium 66, Bethesda, Maryland.

Bettoli, P. W., J. A. Kerns, and G. D. Scholten. 2009. Status of paddlefish in the United States. Pages 23–38 in C. P. Paukert and G. D. Scholten, eds., *Paddlefish management, propagation, and conservation in the 21st century: Building from 20 years of research and management.* American Fisheries Society, Symposium 66, Bethesda, Maryland.

Boere, G. C., and D. A. Stroud. 2006. The flyway concept: What it is and what it isn't. Pages 40–47 in G. C. Boere, C. A. Galbraith, and D. A. Stroud, eds., *Waterbirds around the world.* The Stationery Office, Edinburgh, U.K.

Brown, C. J. D. 1951. The paddlefish in Fort Peck Reservoir, Montana. *Coepia* 3:252.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173–1187.

Chilcote, M. W. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 60:1057–1067.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews* 81:163–182.

Grady, J. M., and B. S. Elkington. 2009. Establishing and maintaining paddlefish populations by stocking. Pages 385–396 in C. P. Paukert and G. D. Scholten, eds., *Paddlefish management, propagation, and conservation in the 21st century: Building from 20 years of research and management.* American Fisheries Society, Symposium 66, Bethesda, Maryland.

Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark–resight data of wintering Canada geese. *Ecology* 72:523–533.

Howell, B. R. 1994. Fitness of hatchery-reared fish for survival in the sea. *Aquaculture and Fisheries Management* 25:3–17.

Jennings, C. A., and S. J. Zigler. 2009. Biology and life history of paddlefish in North America: An update. Pages 1–22 in C. P. Paukert and G. D. Scholten, eds., *Paddlefish management, propagation, and conservation in the 21st century: Building from 20 years of research and management.* American Fisheries Society, Symposium 66, Bethesda, Maryland.

Mestl, G. E., and J. Sorensen. 2009. Joint management of an interjurisdictional paddlefish snag fishery in the Missouri River below Gavins Point Dam, South Dakota and Nebraska. Pages 235–260 in C. P. Paukert and G. D. Scholten, eds., *Paddlefish management, propagation, and conservation in the 21st century: Building from 20 years of research and management.* American Fisheries Society, Symposium 66, Bethesda, Maryland.

Pierce, L. L., B. D. S. Graeb, D. W. Willis, J. S. Sorensen, and M. A. Pegg. 2011. Stocking success of paddlefish in Lake Francis Case, South Dakota: Population characteristics and sport fishery potential. *Transactions of the American Fisheries Society* 140:1359–1369.

Pracheil, B. M. 2010. Multi-scale perspectives on paddlefish populations: implications for conservation and management. Ph.D. dissertation. University of Nebraska–Lincoln, Lincoln, NE.

Scarnecchia, D. L., L. F. Ryckman, Y. Lim, G. Power, B. Schmitz, and V. Riggs. 2006. A long-term program for validation and verification of dentaries for age estimation in the Yellowstone–Sakakawea paddlefish stock. *Transactions of the American Fisheries Society* 135:1086–1094.

Sloss, B. L., R. A. Klumb, and E. J. Heist. 2009. Genetic conservation and paddlefish propagation. Pages 307–327 in C. Paukert and G. Scholten, eds., *Paddlefish management, propagation, and conservation in the 21st century: Building from 20 years of research and management*. American Fisheries Society, Symposium 66, Bethesda, Maryland.

Stancill, W. G., G. R. Jordan, and C. P. Paukert. 2002. Seasonal migration patterns and site fidelity of adult paddlefish in Lake Francis Case, Missouri River. *North American Journal of Fisheries Management* 22:815–824.

Steffensen, K. D., L. A. Powell, and J. D. Koch. 2010. Assessment of pallid sturgeon survival in the Lower Missouri River. *North American Journal of Fisheries Management* 30:671–678.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(Suppl.):120–138.

Wilcove, D. S., and M. Wikelski. 2008. Going, going, gone: Is animal migration disappearing. *PLoS Biology* 6:1361-1364.

Zigler, S., M. Dewey, B. Knights. 2003. Movement and habitat use by radio-tagged paddlefish in the upper Mississippi River and tributaries. *North American Journal of Fisheries Management* 23:189–205.

American paddlefish (*Polyodon spathula*) by Timothy Knepp, U.S. Fish and Wildlife Service
http://digitalmedia.fws.gov/FullRes/natdiglib/8201D6FD-84DC-4C9F-85DDD138790E62B1.jpg

American paddlefish (*Polyodon spathula*) at 60 days of age at the Garrison Dam National Fish Hatchery in Riverdale, North Dakota, in the United States. By the time they are 60 days old, juvenile American paddlefish have assumed the look of an adult paddlefish. Fish this size which are raised in hatcheries can be tagged so they may be identified later in the wild. Photo courtesy U.S. Fish & Wildlife Service.