ESSAY

Olfactory Activation: Imprinting as an Emerging Frontier in the Conservation of Non-Salmonid Migratory Fishes

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A Unifying Approach to Migratory Fish Conservation

There are often stark differences in our understanding, hence management, of anadromous and migratory freshwater fishes. Many of these migrators are compelled to navigate among distinct rearing, feeding, and spawning habitats, yet now require artificial propagation to maintain populations in compromised waterbodies. Besides migratory behavior and population declines, these fishes share olfactory physiology—whether semelparous or iteroparous (Hasler 1966). Knowing when, where, and how olfaction dictates migratory life histories could assist recovery efforts seeking to maximize a species' recruitment to the next generation. This broad understanding has been applied to the enhancement and conservation of semelparous Pacific salmon *Oncorhynchus* spp.

Pacific salmon epitomize the potential of fish olfaction; they memorize, or imprint, the chemical signal of their natal waters during incubation and early rearing. Years later, upon their return from the sea, this chemical memory produces phenomenal homing abilities, allowing the fish to follow a scent trail to their natal freshwater spawning ground, as well as an opportunity for managers to exploit these traits (Hara et al. 1965; Keefer and Caudill 2014). Other fishes may use similar olfactory imprinting to identify natal spawning areas that provide incubation and rearing qualities needed to enhance offspring survival and recruitment. Acknowledging potentially similar olfactory abilities in non-salmonid migratory fishes could provide a unifying, albeit relatively untested, approach to fish conservation via imprinting early life stages. The following essay introduces who these migrators are, the salmon imprinting model, the potential for chemical imprinting in other migratory species, experimental possibilities, and considerations and challenges in applying the sequential chemical imprinting process to non-salmonid fishes.

Non-salmonid migratory freshwater and anadromous fishes with high fidelity spawning movements exist worldwide, from the tropics to the poles (Figure 1; Lucas and Baras 2001). Suckers (Catostomidae), sturgeons (Acipenseridae), minnows (Cyprinidae), shads (Clupeidae), and temperate basses (Moronidae) represent North American iteroparous migrators that use various waterbodies (Figure 2; Table 1). Long-distance spawning migrations often separate offspring from adult habitats to improve recruitment to the next generation, such as spawning far upstream in small tributaries among productive rearing habitats that also offset downstream displacement of drifting larvae after hatching (Billard and Lecointre 2000; Cathcart et al. 2019). Like salmon, these fishes symbolize connected waterways, influence foodwebs, and stimulate culture, anglers, and economies, yet are challenged by overharvest along with pervasive and durable habitat alterations (Holtgren et al. 2007; Childress and McIntyre 2015; Deemer 2020). Annual spawning migrations were exploited by some for personal gain but disregarded by others who fragmented streams with dams or diversions (Cooke et al. 2005). As if dams were not injurious enough to fishes, some biologists even exacerbated the concrete carnage with coincidental rotenone poisonings in hopes of eradicating native migratory suckers and minnows, including the Colorado Pikeminnow *Ptychocheilus lucius*, from Colorado River tributaries during the early 1960s (Wiley 2008). Deliberate or not, overharvest and eliminating critical habitat connections led to governmental conservation listing or fishery regulation of several suckers, sturgeons, minnows, shads, and Striped Bass *Morone saxatilis* (Hendricks et al. 2002; Holtgren et al. 2007; Cathcart et al. 2018; Deemer 2020). Now, to recover populations, conservation stocking often relies on transplanting older, physiologically naïve fish from cultured conditions to natural waters that differ chemically and functionally. Mismatching origin and destination waters of stocked fishes ignores their ability to imprint chemical memories.

Figure 1. An aggregation of Flannelmouth Suckers, a migratory species that exhibits spawning stream fidelity, at a tributary to the Colorado River in Grand Canyon during their spring 2021 spawning migration. Photo credit: David Herasimtschuk, Freshwaters Illustrated.

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Figure 2. Iteroparous migratory fish (from top to bottom; left to right): wild Blue Sucker from the Kansas River in Manhattan, Kansas; hatchery-reared juvenile White Sturgeon from the Kootenai River near the border of British Columbia and Idaho; small adult White Sturgeon from the Willamette River outside Portland, Oregon; wild-spawned larval Razorback Sucker (12 mm SL) from McElmo Creek, a tributary to the San Juan River near Aneth, Utah; hatchery-raised adult Razorback Sucker from the San Juan River; hatchery-raised juvenile Colorado Pikeminnow from the Mancos River, a tributary of the San Juan River outside Shiprock, New Mexico; wild adult Colorado Pikeminnow from the Yampa River in Dinosaur National Monument; wild, adult male Flannelmouth Sucker during spawning season in the Mancos River. Photo credits: the author.

From Salmon to Suckers: an Emerging Frontier

Before exploring the physiology and ecological patterns of non-salmonid fish migrations became fashionable, scientists investigated how olfaction linked Pacific salmon migration to their natal waters (Hara et al. 1965; Cooper et al. 1976; Hasler and Scholz 1983). Early research established the olfactory bulb as the brain's active area in salmon migration (Hara et al. 1965), thyroxine as a critical hormone associated with olfactory imprinting, and long-term olfactory memory could be programmed into cultured fishes. These physiological abilities served as blueprints to "olfactory-aware" hatchery practices designed to aid recovery of diminished salmon populations by enhancing the likelihood of stocked fishes returning to their natal imprinted water signature (Keefer and Caudill 2014; Dittman et al. 2015). These demonstrated olfactory abilities also inspired some scientists to apply salmon imprinting models to other species.

Though still inexhaustive of the diversity that exists, non-salmonid fishes reflecting diverse evolutionary histories have

Table 1. Migration types of select iteroparous fishes in North America. Column headers indicate type of migration where "River" indicates within river migrations, "River-River" indicates fish travel between two or more distinct streams such as those that swim from a mainstem river into a small tributary to spawn. Lake-River indicates adults reside in a lake or reservoir and travel into a stream for spawning. Within "Lake" migrations indicate fishes that perform targeted movements to spawn in a lake or reservoir. This is an inexhaustive list of iteroparous migratory fishes. Superscript numbers correspond to reference for iteroparous migratory fishes.

			Freshwater migrations			
Species	**Scientific name**	**Anadromous**	**River**	**River-River**	**Lake-River**	**Lake**
White Bass[16,18,22]	*Morone chrysops*		✓	✓		✓
Striped Bass[5,10]	*M. saxatilis*	✓				
Lake Sturgeon[3,4,21]	*Acipenser fulvescens*		✓			
White Sturgeon[3,4,26]	*A. transmontanus*	✓	✓			
Flannelmouth Sucker[6]	*Catostomus latipinnis*		✓	✓		
White Sucker [12,14,25,29,30]	*C. commersoni*			✓	✓	
Longnose Sucker[9,14]	*C. catostomus*			✓	✓	
Razorback Sucker[1,7,27,28]	*Xyrauchen texanus*		✓	✓	✓	✓
Blue Sucker[24]	*Cycleptus elongatus*		✓			
Sicklefin Redhorse[13]	*Moxostoma sp.*		✓	✓		
Robust Redhorse [15]	*Moxostoma robustum*		✓	✓		
Colorado Pikeminnow[23]	*Ptychocheilus lucius*		✓	✓		
American Shad[2,11,19]	*Alosa sapidissima*	✓			✓	
Hickory Shad[20]	*A. mediocris*	✓				
Walleye[8,17]	*Sander vitreus*		✓	✓	✓	✓

been used to test salmonid olfaction, homing, and imprinting models. Arthur Hasler (1966) applied salmon olfaction and homing models to experiments on non-salmonid fishes such as lake-spawning White Bass *M. chrysops* and Bluntnose Minnows *Pimephales notatus*, respectively. In the 1990s, the salmonid imprinting model stimulated limited yet insightful research on suckers and sturgeon. Scholz et al. (1991) measured thyroxine concentrations in endangered Razorback Sucker *Xyrauchen texanus* eggs and larvae and estimated the imprinting "critical period" occurred 5–11 days post-fertilization, encompassing hatching or swim-up. Then, Werner and Lannoo (1994) illuminated the olfactory architecture of White Sucker *Catostomus commersoni*, a ubiquitous migrator throughout North American waterways, notably in the Great Lakes. They found neural structures necessary for imprinting are present and develop in a 14-day post-hatch window before, during, and after larval emergence and drift. This development rate is slow compared to the olfactory maturity of salmonids that have much larger eggs (and embryos) and longer static incubation periods at their natal site (e.g., Quinn et al. 2006). Russian Sturgeon *Acipenser gueldenstaedti* also have a critical period for imprinting 10–18 days after hatching (Boiko and Grigor'yan 2002). Decades after these demonstrations of olfactory ability, managers tasked with recovering impaired fish populations have not fully recognized the potential applications of these pioneering studies to conserving migratory fishes. Even so, application cannot precede understanding; there is still much to learn about olfactory and migratory abilities of non-salmonid fishes.

Promising studies have characterized parts of non-salmonid migratory fish physiology and homing behavior; but they are not equally distributed among species and rarely has a species' olfactory structure and performance been fully established. In some cases, surrogate species may be used to fill in the gaps (Table 2). Knowledge gaps remain in our understanding of how species' olfaction, homing, straying, reproduction, and recruitment interact. Migrations with spawning stream fidelity have been well established by tagging studies (e.g., Irving and Modde 2000; Callihan et al. 2015; Cathcart et al. 2019), yet the olfactory abilities, including the spatial resolution of fidelity (Quinn et al. 2006), have been relatively neglected and—as Werner and Lannoo (1994) showed—philopatry or straying largely unsubstantiated (Table 2). For some fishes, the first studies are now decades old with sporadic or no continuation (e.g., the sucker science) while others' olfactory and homing (or philopatric) abilities are just being explored, such as those of Striped Bass and Hickory Shad *Alosa mediocris*, respectively (Deemer 2020; Hill 2020).

Experimental Approaches

Concern for imperiled fishes imprinting and homing innovated *in situ* conservation approaches, where biologists facilitate spawning or rearing habitats in natural, yet often fragmented, waterbodies. Lake Sturgeon *A. fulvescens* conservation efforts in the Great Lakes region have used streamside rearing facilities to enhance larval survival, imprinting, and philopatry (Holtgren et al. 2007). *In situ* efforts combining hatcheries with natural rearing environments induced philopatry via stockings of larval American Shad *A. sapidissima* in altered river networks (Hendricks et al. 2002; Aunins and Olney 2009).

Some *in situ* approaches may need to operate under the hypothesis that olfactory development is slower in many migratory fishes compared to salmon. Therefore, the younger the fish (or fertilized egg) and the longer the time spent in distinct waters during the critical period could allow a higher likelihood of imprinting. For example, simulating sucker spawns by stocking eggs in suitable substrates at reaches far upstream tributaries connected to a lake or main-stem river could be more advantageous than stocking post-hatch larvae at the same location since drift may transport stocked fish out of a distinct tributary imprinting zone and into main-stem stream environments before the olfactory system has developed enough. If applied to Razorback Sucker (Scholz et al.1991), egg stocking could target the critical 5–11-day period post-fertilization of the egg, yet before the emergent larval period.

Alternatives to *in situ* methods exist. Mimicking the chemistry of target waterbodies in cultured conditions could imprint early life stage fishes prior to stocking. Using amino acid combinations that mirror natural conditions has been demonstrated to stimulate homing behavior in salmon species (Shoji et al. 2003; Yamomoto et al. 2010; Bandoh et al. 2011; Ueda 2011). If mimicking a waterbody's chemistry is infeasible, *creating* the imprinting signature via synthetic chemicals (e.g., morpholine) is possible by immersing early life stage fish in the odorous chemical prior to being released into a lake or river and, after fish mature, a drip station delivers that same chemical into the tributary (or site) where fish are desired to spawn (Cooper et al. 1976). Applications of embryonic imprinting were outlined for Pacific salmon (Dittman et al. 2015), but stable environments may prevent hatchery-reared fish from reaching imprinting thresholds as early or as frequently, compared to wild fish (Dittman and Quinn 1996). Further, studies suggest habitat quality can override instinctive homing behavior by hatchery salmon (Dittman et al. 2010; Cram et al. 2013). Experimentally replicating (or creating) water signatures to impart specific chemical memories in cultured iteroparous fishes against variable degrees of habitat quality could gauge their conservation efficacy for non-salmonid fishes.

The Sequential Imprinting Hypothesis

Landscapes drive patterns of habitat use and imprinting, a geobiological feedback which may be compromised in degraded rivers. Functional habitats (e.g., productive spawning habitat near backwaters or low velocity side channels that retain emergent offspring for rearing) are likely key agents of imprinting similar to the guideposts of different, yet connected, habitats (e.g., streams, lakes, sloughs) encountered by young salmon in their natal watershed that become progressively etched into their olfactory senses as they incubate, emerge, rear, and then migrate to the sea (Dittman and Quinn 1996). This is known as the sequential imprinting hypothesis and may be a useful framework for understanding olfactory processes of migratory fishes with mobile young, such as those transported downstream by drift (Dittman et al. 2015). Progressively imprinting early life stages of fishes in field and lab settings could tailor olfactory activation methods to functional habitats (those that exist for the right time in the right place). Alternatively, promoting habitats that may impart critical chemical memories while also improving condition, thus survival, of young fish could be another tool to accommodate the sequential imprinting hypothesis. A promising example of how habitat restoration may accommodate parts of the sequential imprinting hypothesis in non-salmonid

Table 2. Inexhaustive overview of olfaction, homing, and conservation strategies toward select migratory iteroparous fishes in North America. Codes are as follows: study (or studies) performed or habitual practices (X), surrogates used (Xs), juveniles stocked (J), and larvae stocked (L). Rearing habitats indicate artificially created and managed habitats that seek to enhance specific parts of species. Straying (S in the Fidelity column) was so rarely considered that it did not warrant a column, though Doherty et al. (2010) found evidence of White Sucker using multiple streams during a spawning season, Hayden et al. (2011) showed White Bass spawning populations are linked by stray fish, Hendricks et al. (2002) found evidence of rare straying events by American Shad, and Chen et al. (2020) addressed straying in Walleye.

	Olfactory processes				*Homing*		*Conservation*			
Species	**Structure**	**Cues**	**Imprint**	**Critical period**	**Fidelity**	**Philopatry**	**Early life stage stocking**	**Hatchery rearing**	***In situ* rearing**	**Rearing habitats**
White Bass					XS	X				
Striped Bass		X			X		J	X[1]		
Lake Sturgeon	Xs		Xs	Xs	X	X	J	X[2]	X	
White Sturgeon	Xs		Xs	Xs			J	X[3]		
Flannelmouth Sucker					X			X[4]		
White Sucker	X			X	XS					
Longnose Sucker					X					
Razorback Sucker				X	X			X[5]		X
Blue Sucker					X					
Sicklefin Redhorse					X			X[6]		
Robust Redhorse					X			X[7]		
Colorado Pikeminnow					X			X[8]		
American Shad		X			XS		L	X[9]		
Hickory Shad					X	X		X		
Walleye					XS	X				

[1] Joseph Manning Hatchery, Maryland Department of Natural Resources.

[2] Streamside rearing facility, Little River Band of Ottawa Indians.

[3] Kootenai Tribal Sturgeon Hatchery, Kootenai Tribe, Bonners Ferry, Idaho.

[4] J.W. Mumma Native Aquatic Species Restoration Facility, Colorado Parks and Wildlife, Alamosa, Colorado.

[5] Ouray National Fish Hatchery (NFH) – Grand Valley Unit (Grand Junction, CO) and Uvalde NFH (Uvalde, Texas), U.S. Fish and Wildlife Service.

[6] Conservation Fisheries, Inc., Knoxville, Tennessee.

[7] Warm Springs Hatchery, U.S. Fish and Wildlife Service, Warm Springs, Georgia.

[8] Southwestern Native Aquatic Resources and Recovery Center, U.S. Fish and Wildlife Service, Dexter, New Mexico.

[9] Van Dyke Hatchery, Pennsylvania Fish and Boat Commission, Port Royal, Pennsylvania (hatchery operations ceased in 2018).

fishes is in Utah, where biologists and engineers are reconnecting floodplains and wetlands with the Green River to entrain larval Razorback Sucker and provide better rearing habitat proximate to their spawning locations (Breen 2016; Caruso et al. 2019).

Conclusion

Migratory fish population declines have motivated conservation efforts, yet government protections and current management practices have failed to recover many populations (Cooke et al. 2005; Holtgren et al. 2007; Day et al. 2017). Reevaluating conservation stocking strategies, further olfactory-focused research, and patience are needed. Stocking (eggs, larvae, juveniles, or adults) should not be viewed as a panacea where just any fish from anywhere can fit into a stream; it can be a precise tool if techniques match a fish's ability to the riverscape. By hacking a species' innate navigation system, biologists could fill in knowledge gaps about a species' early development, movement ecology, fates (e.g., recruitment bottlenecks, "artificial" spawning migrations), and innovate management applications. However, with older ages at first maturity (2 to >6 years for some suckers or shads, >10 years for sturgeons) and skipped spawns, patience may be the ultimate challenge to employing olfactory approaches for fish conservation (Billard and Lecointre 2000; Hendricks et al. 2002; Doherty et al. 2010; Day et al. 2017).

Imprinting processes must be considered to better understand and conserve *all* migratory fishes. Simple repatriation of fish may fail to honor the complex interplay of water chemistry and chemical memories that enable migratory processes ultimately impacting spawning, survival, and recruitment. Salmon, suckers, sturgeons, shads, and Striped Bass are a bricolage when viewed through the chaotic, discriminating lenses of their divergent evolution, landscapes, life histories and managers; the focused lens unifying them is the olfactory underpinning to their migrations.

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