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Notes on Pacific salmon olfactory imprinting, and the effects of transportation and water diversion on homing as they may pertain to McCloud River winter-run Chinook salmon

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1.0. Introduction

The success of volitional passage projects to facilitate salmon reintroduction, and to some extent "trap and haul" projects at juvenile or adult stages, may hinge on both the physical environments (e.g., water temperature, discharge, and velocity) and the migratory behavior of the fish. Specifically, in the case of upper Sacramento River system Chinook salmon, several things must occur. First, the fish must learn appropriate chemical traces early in life while feeding in and migrating through the McCloud River into the head of Shasta Reservoir. They must then make their way, with or without human assistance, through the reservoir, into and down the Sacramento River, through San Francisco Bay, and out into the Pacific Ocean. Those that survive must reverse their pathways as adults returning to spawn.

The processes of migration and homing by salmon are remarkable, and any disruption in the learning process prior to and during migration, or modifications of water sources confronting returning adults, only complicate their task of getting home. These challenges are real and must be considered as part of the overall process of planning any human activities on behalf of the salmon. However, the outcomes will be determined by the fish, whose behavior is difficult to predict and control. This document briefly reviews some of the scientific literature on how salmon learn (i.e., "imprint") on the odors of their natal stream, how transportation can affect this process, and how homeward migration proceeds in fish with some disruption either in their experience during early life stages or by diversions of water experienced as adults. With respect to McCloud River salmon, some of the key questions deal with the following: 1) transportation of juveniles to circumvent predation risk in Shasta Reservoir and facilitate passage at dams; 2) the extent to which flow and temperature conditions along the return route will be deemed attractive to salmon, even if these conditions have been learned; and 3) the possible effects of diversion of McCloud River water into the Pit River on migratory behavior of adult salmon entering Shasta Reservoir.

2.0. Background and Literature Review

Under natural circumstances, juvenile salmon emerge from redds in stream or lake habitats and move about in freshwater, as the ecology of their species and population dictate, before migrating to sea (Quinn 2018). At one or more times during their lives in, and migration from, freshwater habitats, they learn the chemical signature of the waters in which they live and migrate. They store these odor memories and use them later as maturing adults, transitioning from ocean to estuary to river habitat and returning to spawn in their natal sites (though a small and variable fraction strays and spawns elsewhere).

Experimental disruptions of this natural sequence by transporting salmon from one hatchery to another prior to release (Donaldson and Allen 1957; Candy and Beacham 2000; see Lister et al. 1981 for an extensive review of many published and unpublished reports on transfers between sites) or from a hatchery to a point along the migration corridor (Quinn et al. 1989a) present a complex picture of the imprinting process. Salmon taken from one hatchery as parr or smolts and brought to another hatchery on a different watershed for release tend to return as adults to the point of release rather than the site where they were raised (e.g., Donaldson and Allen 1957; Johnson et al. 1990). Fish moved from a hatchery and released as smolts at downriver locations in the natal river or its tributaries also tend to return to the release sites (e.g., steelhead: Wagner 1969; Cramer 1981; Slaney et al. 1993; Kenaston et al. 2001). Salmon taken from a hatchery prior to migration and released downstream along part of the migratory route (e.g., around dams on the Columbia River) tend to return to the point of release or that vicinity (Vreeland et al. 1975), even if the odors from the natal hatchery are available nearby (Quinn et al. 1989a; Brannon and Quinn 1990; Solazzi et al. 1991). However, if the salmon are captured during their migration and transported farther downstream (e.g., past dams on the Columbia River or Snake River) they tend to return to their natal site as adults (Ebel et al. 1973; Slatick et al. 1975; Ebel 1980).

Taken together, these results support the conclusion that olfactory imprinting in salmon is closely linked with migration. Indeed, the act of migration may be necessary for imprinting to occur (Dittman et al. 1996). Moreover, salmon seem to imprint sequentially

rather than only once as smolts (e.g., sockeye salmon: Quinn et al. 2006; Havey et al. 2017; Barnett et al. 2019; Atlantic salmon: Armstrong et al. 2022). The idea of sequential imprinting has been considered for some time (Harden-Jones 1968), and it now seems clear that salmon probably imprint at several ecologically important times in their lives, corresponding to periods of migration. The first is at or before emergence from the gravel near the redd site, and the last may be the point of seawater transition in the estuary or nearshore marine environment. During downstream migration, the exposure to novel water, as might occur at the confluence of two rivers, seems to stimulate transient increases in the thyroid hormones associated with olfactory learning and also the parr-smolt transformation (e.g., Grau et al. 1985; Hoffnagle and Fivizzani 1990). When adult salmon return to spawn, their migrations at sea are controlled by mechanisms that function in open water (Putman et al. 2013), but when they reach coastal waters, they shift to olfaction-based homing mechanisms in some poorly understood period of interface between mechanisms (Madison et al. 1972; Stasko et al. 1976; Døving et al. 1985; Quinn et al. 1989b). Salmon are generally believed to use what is known as a "sign-stimulus" process for using odors to locate their home stream. That is, detection and recognition of an imprinted odor triggers upstream swimming (Johnsen 1982; Johnsen and Hasler 1980). This is different from, for example, a system in which they might seek gradients of odors. However, they can experience "false attraction" if presented with natal odors out of sequence or in the wrong place (as might occur with a diversion), as described later in this summary.

It is not known what specific chemicals remain sufficiently similar between seasons and years that allow salmon to identify their natal waters. Salmon typically return to spawn several years after leaving their natal stream and migrate during a different season from that when they last experienced their home waters as juveniles, yet they can discern their home odors despite these differences. Juvenile salmonids can discriminate the odors of their own population from other populations (Courtenay et al. 1997; Groot et al. 1986; Quinn and Tolson 1986) and tend to be attracted to them and to species-specific odors in general. There is a building scientific literature supporting the hypothesis that unique combinations of amino acids in streams provide the basis for discrimination (e.g., Yamamoto and Ueda 2009; Yamamoto et al. 2010, 2013; Dittman et al. 2022; Minkoff et

al. 2023). Others have suggested that minerals associated with the unique geology of different rivers might provide stable olfactory cues, and there is some evidence that such compounds may act as odorants (Bodznick 1978), but their role in homing has not been demonstrated. This uncertainty in the chemical nature of the key odorants makes it difficult to project how salmon will react to alterations in water sources associated with some hypothetical future action.

Under normal circumstances, almost all salmon that survive to maturity successfully retrace the sequence of odors and return to the vicinity of their emergence site. It is unclear how they avoid distraction by chemicals that are present on their return migration but were absent (or present in different absolute or relative concentrations) when they imprinted. It is equally unclear how they are not confused by the absence of chemicals on the return that were present during imprinting. Even the massive changes in water quality associated with the eruption of Mt. St. Helens in Washington did not mask the home odors, though the salmon seemed inclined to avoid the ash-laden water (Leider 1989; Whitman et al. 1982). In addition to changes in stream chemistry between seasons and years, the amino acid profiles in a stream can vary greatly over the course of the spawning run (Dittman et al. 2022), yet salmon homing is not affected by these changes.

In conclusion, the literature on salmon homing and imprinting is vast and not without some contradictions. However, the overall body of knowledge is consistent with the hypothesis that salmon imprint not only at the smolt transformation period but sequentially at a series of earlier life history transitions that are marked by migration. Of these migrations, the smolt period is normally a critical one and has been most clearly demonstrated experimentally but imprinting also occurs at emergence from the gravel and likely other times as well. The very act of migration itself seems to be important or essential in the imprinting process because fish transported from a hatchery tend to return to the release site whereas those caught during their migration and transported tend to return to the natal site, albeit with some reduction in homing (Quinn 1994; Chapman et al. 1997; Bond et al. 2017).

3.0. Application to Sacramento River Chinook salmon conservation and restoration

The migration of juvenile and adult winter-run Chinook salmon between the free-flowing Sacramento River and the McCloud River, prevented for many decades by impassable dams, presents many challenges. Engineering and hydraulic solutions must be proposed and presented in some detail before estimates might be made of how the fish might respond, and even then such estimates will be uncertain. However, at present, some points might be made, derived from the background information presented previously.

First, if Chinook salmon spawn naturally, or if their offspring emerge from conventional remote site incubators or some modified (e.g., more natural) stream-side incubator fed by water from the McCloud River and then migrate volitionally downstream, there is every reason to expect them to imprint on the natural odors of the river. However, if they were captured at emergence and transported, there would be a risk of incomplete imprinting and a tendency to return to the release site.

Second, if juvenile salmon migrate to and are then captured at the head of the McCloud Arm of the Shasta Reservoir for transportation rather than allowed to migrate volitionally, there is some risk of impaired imprinting. However, the fact that they would have already initiated migration would work in their favor. Further investigation of the natural patterns of smolt physiology and migration timing of winter-run Chinook salmon would be needed to better consider this matter. If the reservoir is deemed to be too dangerous for volitional passage (e.g., from high temperatures, predator densities, difficulties in finding the exit, or other considerations), the fish would presumably have to either be transported or migrate via some flume or other conduit to their downstream route. That route might be, for example, the Dry Creek–Cow Creek system. If so, then they would imprint on those odors during downstream migration and thence to the confluence with the Sacramento River, through San Francisco Bay, and out to sea.

Third, salmon surviving their period at sea would ascend the Sacramento River and likely detect the confluence with Cow Creek if they had migrated down it years earlier. It is unclear how salmon strike a balance between ascending a stream that they recognize as home and avoiding one that seems unsuitable. Westley et al. (2015) examined coded wire

tagging data for stream-type Chinook salmon in the Columbia River basin and found that higher temperatures in the natal subbasin and the Columbia River were associated with higher rates of straying. Moreover, lower density of adults was associated with higher rates of straying, consistent with several other studies (reviewed in Berdahl et al. 2016). Thus, warm water and low adult density both seem to reduce the proportion of salmon that home, though they do not prevent it entirely. The effects of flow *per se* (i.e., as distinct from links to temperature) are less clear but are under investigation (Westley et al. in review).

Fourth, the diversion of water from the McCloud River to the Pit River (estimated at approximately 600 to 800 cubic feet per second) poses additional complications for returning salmon. Hypothetically, if they were to ascend the Sacramento River to Cow Creek and up Dry Creek and into Shasta Reservoir, they would be in closer proximity to the Pit River than to the McCloud River. Water diversion projects have been completed or proposed elsewhere, and in some cases "false attraction" is raised as a concern because the temperature, flow, odors, or some other property of one water source might attract fish. Such projects are not replicable, like laboratory experiments; each is unique to the situation where it was planned or completed. Consequently, one has to take a "weight of evidence" approach when drawing conclusions from these kinds of studies or proposals.

An example of the effects of water diversion on salmon homing was provided by a study of adult sockeye and pink salmon returning to Seton Creek, a tributary of the Fraser River in British Columbia (Fretwell 1989; see maps from Bett et al. 2018 at the end of this report for reference). After completion of a hydroelectric project at this site, it was observed that diversion of Seton Lake water (approximately 90%) through the hydroelectric facility disrupted the normal homing migration because salmon were attracted to the tailrace of the power plant rather than their natal stream. A combination of radio telemetry studies under different diversion regimes and laboratory experiments indicated that salmon preferred the tailrace water containing 100% home stream water (diverted for power generation) versus the natural stream channel containing home water diluted with significant amounts of water from a non-natal stream, Cayoosh Creek. Seasonal alterations in flow regimes and the composition of water in the natal stream

channel reduced the disruptive effects of the hydroelectric project (Fretwell 1989). These studies demonstrated that migrating adult salmon can distinguish between different dilutions of home stream water, and that the water containing the higher proportion of home stream water was more attractive. The study also revealed that water diversion can strongly affect salmon homing and may be taken as a warning that effects on migratory behavior may be complex.

Subsequent studies were conducted in the Seton – Anderson system after Fretwell's (1989) initial. Bett et al. (2018) conducted riverside experiments and concluded that "… sockeye populations exhibited behavioural preferences for pure natal water when compared with various levels of diluted natal water, whereas pink salmon … appeared unaffected by natal dilution." [p. 1151]. Drenner et al. (2018) conducted radio tracking on sockeye salmon in this system and used experimental flow manipulations to determine whether their behavior could be modified. They concluded [p. 498],

> "Current management guidelines call for maintaining >80% natal water concentrations in the Seton River during Gates Creek sockeye salmon migrations. This study tested 72% versus 92% natal water concentrations and, thus, cannot specifically confirm the >80% natal water management target. Nonetheless, these results provide evidence that dilution of natal water in the Seton River can influence behaviour of upriver-migrating sockeye salmon and provide some of the first evidence that free-swimming salmon respond behaviourally to altered olfactory cues in a large river system modified by hydropower operations. Overall, the impacts of altered olfactory cues on fish because of human activities, such as river impoundment and diversions, should be more widely considered, but, as evidenced herein, these issues can often be mitigated or avoided altogether given proper design and management of hydropower facilities."

A second key variable is whether the diversion of McCloud River water through its conduit to the Pit River will impart odors to the water. The ability of salmon to detect differences in odors stretches the imagination, yet they routinely perform truly remarkable feats of discrimination. For example, the water that supplied the University of Washington's salmon hatchery was pumped straight from the surface of the Lake

Washington ship canal, through the hatchery's pipes and ponds, and back into the ship canal less than 20 m downstream from the intake. Nevertheless, the ship canal water, containing the diverse odors of the entire Lake Washington basin, was altered enough during this quick pass through the hatchery for salmon to detect it and enter the hatchery rather than continue swimming up the ship canal. Any odors imparted during the water's transit to the Pit River, or by the Pit River itself and its tributaries, might tend to reduce its attractiveness to salmon, and increase the chances that they would locate and ascend the McCloud River.

4.0 Conclusion

It is difficult to predict the behavior of wild animals under any circumstance and especially something as complex as salmon homing under conditions such as those being proposed. The so-called Harvard Law (original source unknown) states that "Under the most rigorously controlled conditions of pressure, temperature, volume, humidity, and other variables, any experimental organism will do as it damn well pleases." The engineering aspects of a partial or complete volition passage option for McCloud River winter-run Chinook salmon are complicated in many ways, but ultimately it is the fish who will pass judgement, and they keep their cards close.

5.0. References

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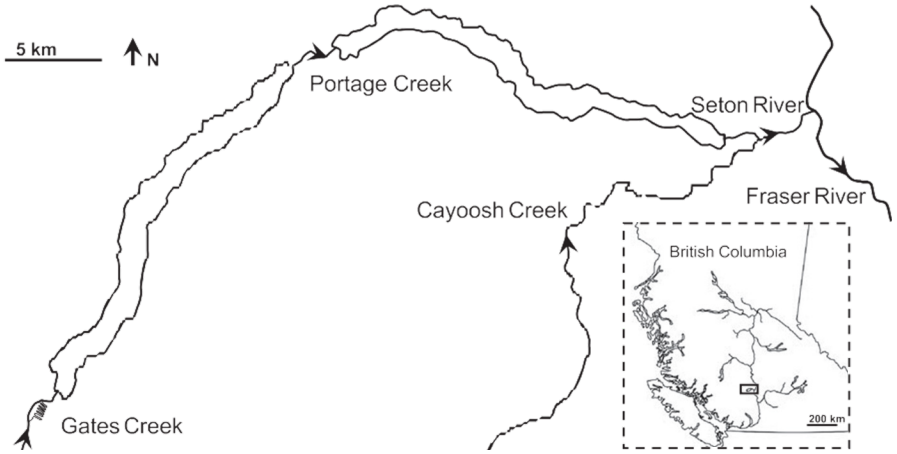

FIGURE 1. Map of study area within British Columbia's Fraser River system (inset). Sockeye salmon spawn in Gates Creek and Portage Creek, whereas pink salmon spawn throughout the region [from Bett et al. 2018].

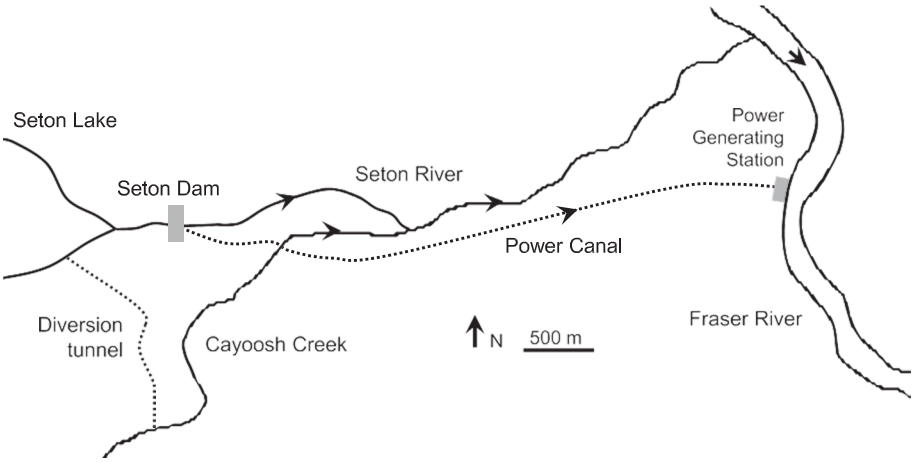

FIGURE 2. Diversion of water from the outlet of Seton Lake down a power canal. Water in the power canal exits through a generating station into the Fraser River, providing an attractive source of water to adult salmon migrating upstream. [from Bett et al. 2018].