Why and How Do Salmon Migrate?

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Animal migration is a complex behaviour that is characteristic to most animals on Earth. Salmon has one of the most impressive migratory task. Their life cycle starts in rivers, followed a few months later (however varies across species) by migration to the ocean. Once full development occurs, they would return to their spawning place (homing). Besides the travelling distance, which can be thousands of kilometres, they also put themselves at risk of being prey for bears, bald eagles and fishermen (Dittman & Quinn, 1996). This essay will attempt to explain the causes for salmon migration and how they succeed in doing this.

We will start with briefly presenting the causes of salmon migration. Then we will provide evidence for salmon navigation, focusing on the olfactory and magnetoreception hypotheses.

The most likely explanation for the salmon migration from the river to the ocean is that the ocean provides more food supplies. This is illustrated by a decreased body weight of sockeye salmon that stay in rivers all year round compared to oceangoing sockeye (Gross, Coleman & McDowall, 1988; Freeman, 2018). The reverse migration, homing, is caused by salmon's need to breed. Spawning grounds of the river are thought to provide a more protected environment, with fewer predators, than the ocean, which increases the likelihood for successful reproduction.

Considering that salmon can distance thousands of miles from their spawning place, it is remarkable that they are able to return to the same very place even after years of being away. A possible solution to the puzzle of salmon homing is offered by the olfactory hypothesis (OH), which states that salmon use the olfactory cues to find their spawning place.

The first pieces of evidence for OH come from Hasler and Wisby (1951) who used instrumental conditioning in salmon (with food as reward and electric shock as punishment) to discriminate between waters from different streams. Once the association was learnt, salmon had their nose blocked. As expected, they were unable to perform the task anymore, which suggests that odours were the discerning cue between waters. They also found that salmon could identify water from the same stream from different seasons, which suggests that the element identified in water is long-lasting.

An insight in how salmon remember the odours of their natal place is provided by Bett et al. (2016). They exposed pink salmon in their first developmental stage (alevin) to phenetyl alcohol. When salmon reached adulthood, they had to choose between two sides of a water tank: one with phenetyl alcohol, the second without it. The results showed that salmon preferred significantly more the phenetyl alcohol water to the control water. This provides evidence that the odour memorisation is due to imprinting at an early stage of development, before heading to the ocean.

The OH also received support from field experiments. Wisby and Hasler (1954) performed their experiment on a small Y-shaped tributary with two branches: Issaquah Creek and its East Fork. They captured adult spawning salmons from both branches. They then divided fish from each branch in two treatment categories: the control group which were only tagged; the second group that was made anosmic by plugging nares with cotton. After treatment, all were released at the confluence of the branches, one mile away, and monitored how many would return to the initial site. As Table 1 shows, there were more controls that returned to their initial site than the anosmics, which demonstrates that smell was used for orientation.

Thus far, the presented evidence demonstrates salmon's potential to use river's olfactory cues for navigation. However, OH does not explain how they reach the vicinity of river as it is highly unlikely that salmon can sense the natal place odours at hundreds of km in the ocean.

Fortunately, the impasse can be overcome with the magnetoreception hypothesis (MRH). This states that salmon imprint on the geomagnetic values (GMV) of their spawning place, and during homing they follow the large-scale magnetic gradients to relocate the same GMV (Putman, Jenkins, Michielsens & Noakes, 2014). The GMV that salmon would use are the intensity and inclination angle of Earth's magnetic field. A few studies discovered large numbers of single-domain magnetite particles in salmon's fore part of the body that can be used for magnetoreception (Kirschvink, Walker, Chang, Dizon & Peterson, 1985; Walker, Quinn, Kirschvink & Groot, 1988). Thus, Lohmann, Putman and Lohmann (2008) propose that salmon use magnetoreception in the ocean and once their river's mouth is reached it should be close enough to sense the familiar olfactory cues.

There are concerns about MRH because the GMV for a specific geographic point are constantly changing – called the magnetic drift – making the reliance on the same GMV misleading. Lohmann et al. (2008) calculated the navigational errors due to magnetic drift for salmon that aimed the tributaries of the Columbia River in Washington. They were averaged to approximately six km over the past century if the fish imprinted on the inclination angle at the mouth of the river and approximately 31 km if they imprinted on intensity. Authors suggest that these errors permit to at least identify the mouth of the river.

Far from being a problem, the magnetic drift was used to consolidate MRH. Putman et al. (2014) analysed the homing route of pink and sockeye salmon to Fraser River (spawning place) from 1950s to date and the magnetic drift for this period. To get to the mouth of Fraser River, fish must detour the Vancouver Island, which can be done either through the Queen Charlotte strait (QC) or Juan de Fuca strait (JdF) (see Figure 1). Researchers found a correlational relationship between the homing routes chosen (either QC or JdF) and the magnetic drift. This result suggests that salmon follow the path that is shorter to the imprinted geomagnetic location, even if the other route would be faster to the river mouth.

In conclusion, there is strong evidence for OH and convincing evidence for MRH. Fortunately, for salmon, they do not contradict each other and can be combine, as suggested by Lohman et al. (2008), in a biphasic navigation.

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Table 1

Number of Salmon (Percentage) Recaptured

		Recapture Site	
Treatment	Capture Site	Issaquah	East Fork
	Issaquah	46 (100)	0 (0)
Control	East Fork	8 (30)	19 (70)
	Issaquah	39 (76)	12 (24)
Anosmic	East Fork	16 (84)	3 (16)

Note. Each row represents the total number of salmon from one treatment condition (i.e. Control or Anosmic) and one capture site (i.e. Issaquah or East Fork). From *Mechanisms of Homing: Imprinting, Genetics, and Pheromones*. (2018). *Courses.washington.edu*. From http://courses.washington.edu/fish450/Lecture%20PDFs/home_stray_2.pdf

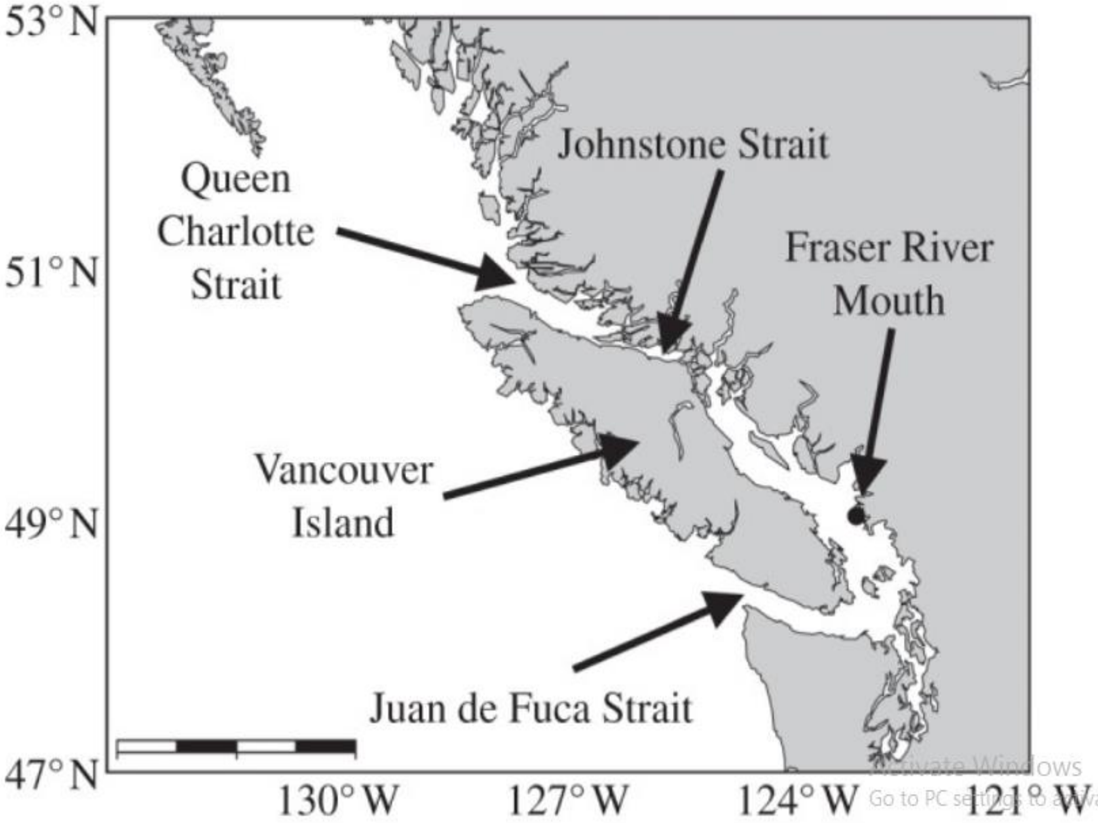

Figure 1. Salmon routes to Fraser River during homing. Scale bar is 225 km. Adapted from 'Geomagnetic imprinting predicts spatio-temporal variation in homing migration of pink and sockeye salmon' by N. Putman, E. Jenkins, C. Michielsens, and D. Noakes, 2014, *Journal of The Royal Society Interface, 11*(99). Copyright 2014 by the Royal Society.