

LITERARY REVIEW: GENETIC BASIS OF MIGRATION

by

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Abstract:

Many species of animals undertake long-distance migrations to take advantage of seasonal resources that are not present within their home ranges. The goal of this paper is to examine research that is investigating genes and alleles that differ between resident and anadromous (migratory population) salmonids – salmon, trout, and charr. Research had indicated so far that there appears to be a positive correlation between the migratory patterns of parental trout and the migratory patterns of their offspring, suggesting underlying genetic factors involved in the development of either migrating or staying resident. Various regions of their genome have been identified as involved in the process of migration in rainbow trout. However, it is still unknown which specific polymorphisms within these genes are causing the variation in migratory behavior. Locating polymorphisms that vary between resident and migrant trout and then genotyping them in many individuals will help determine the genetic basis of migration and be useful in conservation studies as many populations of migratory trout are decreasing at alarming rates. Questions to be explored in this paper include: What is migration? What indicates if a salmon will migrate or not? What role does the environment play on gene expression? What specific genetic rearrangements and SNPs are playing a role in determining migratory behavior and how heritable are they?

Introduction:

Migration can be defined as the movement of individuals over a long range for a temporary period before returning back home. There are other types of movement such as dispersal where species move to set up new territories, or movement associated with finding resources (foraging), but these are different from migration in that they are over short distances, small timescales, and often do not have a set directionality (Dingle 2007). There is also movement called commuting where an individual will travel to a specific place each day to collect resources; this is typically a distance further than what we could consider foraging, but, like foraging is a regular movement (Dingle 2007). There is another movement associated with long distance locomotion called ranging, but this is different from migration in that the population settles in a new place and does not return to their native home (Dingle 2007). It is important for studies to be specific about the type of movement being investigated because species can show two or more locomotion.

A full understanding of migration encompasses its mechanisms and functions. According to Dingle, there are four concepts that are required for a movement to be considered migration: 1) movement that is persistent and undistracted, 2) the relocation is on a much greater scale than movement in normal daily activities, 3) seasonal movement is due to resources being favorable or unfavorable, and 4) the movement extends throughout multiple individuals within a population. There is debate whether migration should be defined within the individual where it would be considered a behavior or within a group of individuals where it would be considered a function (Dingle 2007). This is an important distinction when decisions regarding conservation are being discussed because when a larger amount of the population migrates, there is greater implications with respect to conservation and allocating resources to help increase populations,

rather than if it is just an individual or two. Regardless, migration is recognized as an adaptation driven by the availability of resources in various locations.

Despite migration being a very widespread and observed phenomena, it is quickly disappearing due to human interference. There are four ways, as described by Wilcove, that are causing this disappearance: habitat destruction, creation of obstacles, overexploitation, and climate change. One of the greatest inhibitions we have seen to migration concerns migratory fishes and aquatic organisms, where blocking of drainages by dams has an enormous impact on the ability of migratory individuals to complete their life-cycles.

Many species of animals undertake long-distance migrations to take advantage of seasonal resources that are not present within their home ranges. The goal of this paper is to examine research that is investigating genes and alleles that differ between resident and anadromous (migratory population) salmonids – salmon, trout, and charr. Research had indicated so far that there appears to be a positive correlation between the migratory patterns of parental trout and the migratory patterns of their offspring, suggesting underlying genetic factors involved in the development of either migrating or staying resident. Various regions of their genome have been identified as involved in the process of migration in rainbow trout. However, it is still unknown which specific polymorphisms within these genes are causing the variation in migratory behavior. Locating polymorphisms that vary between resident and migrant trout and then genotyping them in many individuals will help determine the genetic basis of migration and be useful in conservation studies as many populations of migratory trout are decreasing at alarming rates. Questions to be explored in this paper include: What is migration? What indicates if a

salmon will migrate or not? What role does the environment play on gene expression? What specific genetic rearrangements and SNPs are playing a role in determining migratory behavior and how heritable are they?

Migration:

Since migration is considered heritable due to the genetic correlations, it is highly likely that it responds to natural selection and is adaptive (Hecht et al 2015). In looking at migration holistically, there are a variety of forces acting on determining if an individual stays resident or migrates, including gene expression, environmental influence, the physical ability of the individual, and barriers to completing migration (Dingle 2007). These factors can lead to issues affecting population density, ability for organisms to access materials, and mating potential if migratory individuals are not capable of successfully returning to spawn.

Migration is specifically important because it provides the resources for ecological properties and services. For example, when salmon migrate from the ocean, they bring nutrients from the ocean to their home lake which gives phosphorus and nitrogen to the zooplankton and phytoplankton which in turn provides food for smaller fish (Wilcove 2008). Since there are more nutrients in the ocean it is more common for females to migrate than males because they need more energy to create gametes than males (Hale et al 2013). The construction of dams, overfishing, irrigation causing low water levels, logging, and grazing by livestock have caused migratory salmon populations to fall drastically (Wilcove 2008). This has had large negative effects on the amount of phosphorus and nitrogen available with worrying consequences on the health of other ecosystems in the Pacific Northwest.

Salmonid species are interesting to study in terms of migration because most species exhibit two different life histories. Like most migratory species, the adoption of the different life histories is due to a combination of genetic and environmental effects, making migratory life history development a quantitative trait (Weinstein et al 2019). The first is a resident life history where the fish will live its entire life in a freshwater system. The second is an anadromous life history where a juvenile fish will develop into a salmonid that can sustain being in sea water and then will migrate to a marine water system. It will return after two to four years to their natal fresh water to spawn. Anadromous population use the nutrients in the ocean as resources for growth which makes them more fit and capable of producing many more gametes compared to resident individuals as resources in northern freshwater streams tend to be low when compared to the ocean (Waples et al 2019).

When comparing anadromous and resident species, there tends to be a difference in morphology and physiology due to gene expression and their response to environmental cues. These changes increase a species ability for long distance movement. Examples of this would be longer wings for birds or insects and a greater streamline body-shape for fish (Dingle 2007). These morphological changes also depend on the season of migration. Many species of salmon and trout are unusual in that they have returning shoals – known as spawning runs – at different times of the year. For example, winter and spring migrants typically have high fat contents, early spawning, and small body sizes, whereas summer and fall migrants have low fat contents, late spawning, and large bodies (Harringmeyer et al 2020).

In order to migrate salmon and trout must go through a demanding process called smoltification. Smoltification involves multiple morphological changes including elongation of their body to streamline their profile allowing for less water drag, lower body condition (the measure relationship between body length and weight), deposition of guanine and hypoxanthine of the skin turning it reflective silver making them more adapted to marine environments and altering their internal physiology to cope with the osmoregulatory demands of seawater (Hecht et al 2015). As mentioned above, these changes are linked to both environmental cues and changes in gene expression. In the photo below you can see the differences between resident (B) and smolts



Although many species of salmon, trout, and charr exhibit variation in migratory behavior, a lot of research has been dedicated to understanding the genetic basis of migration in rainbow trout (*Oncorhynchus mykiss*) as 1) both life histories are frequently found in the same water system, and 2) it is well known that the development of the different life histories has a strong genetic component (Hecht et al. 2015) This helps identify genes that have adaptive significance, which

are heritable, and if there are any significant patterns of genetic divergence between the two life histories (Hale et al. 2013).

Genomics:

Genomics is using genome-wide genetic data to understand questions by using conceptual and quantitative approaches that would be impossible on a gene-by-gene basis (Waples et al 2019). This allows us to use genetic information about the structure and function of the genome to solve problems in health and conservation fields. An important use of genomics is linking genes with phenotypic traits. One way the scientist are able to identify these differences between populations are looking at single nucleotide polymorphisms (SNPs) that are changes in a single nucleotide when looking between two loci that could influence phenotypic traits. Often times there are multiple SNPs within the same locus that causes a phenotypic effect which allows geneticists to determine if an allele is associated with migration or residency.

Genomics suggests that different large scale polymorphism such as chromosomal inversions, deletions, translocations, fusions, and fissions may also be important to the development of different life histories. Although the frequency of these rearrangements does appear to vary on a population level, suggesting that a) there are population specific genetic effects (Weinstein et al 2019) and b) that chromosomal inversions are variable within a species. For example, a chromosome inversion has been found on chromosome 5 in rainbow trout with the inverted version associated with differences in salinity tolerance, migratory behavior, crypsis and development rate (Waples et al 2019). These phenotypes may well be adaptive and responding to

the effects of selection. Interest in inversions such as this, comes from the inability of heterozygous individuals to undergo homologous recombination (Weinstein et al 2019). Over time, this results in two conserved alleles making it easier to predict the ultimate life history of an individual based on their chromosome five allele. Kelson found that an increase in percentage of SNPs in the inverted version results in rapid early growth and the salmon will be a resident. Based on these findings we can say that early life growth is associated with adopting a resident life history. However, evidence from several populations suggests that other regions of the genome are connected to smoltification and migration. This means that the chromosome five inversion is not a fool proof way to determine migration history because the decision can be context dependent as we discussed above.

When looking at genomics and migratory behavior there are two different ways they could be related. The first is inherited or direct genetic control. This would mean that the alleles within the genome determine, solely, the development of the individual via differences in the protein produced, or by regulating differential gene expression between the migratory and resident phenotypes. The second is indirect genetic control, where the environment interacts with physiological traits and that would determine if migration is an option or not. Indirect genetic control has more evolutionary benefits because the species would have more phenotypic plasticity, which is where an individual, depending on the environment, could decide to migrate or not (Kelson et al 2020). An environment that would favor migration is one with little resources and high competition. In the case where there is a lot of resources and little competition, it would make sense for the species not to expend the energy to migrate. Kelson in turn

determined that genetics and environment directly influences the physiological condition of an individual with then directly influences migratory behavior.

Specifically looking at traits that have importance either evolutionarily or ecologically helps identify genes that are adaptive and are functionally relevant (Waples et al 2019). Some of this data now includes an understanding of the genetic basis of specific traits related to smoltification. On chromosome 12, there are alleles associated with several important traits, including body condition, growth rate, body length, and body weight. Similarly, alleles have been found on chromosome 14 that are associate with growth weight, body condition, anterior body length, dorsal fin base length, and snout shape. These results suggest two things; 1) that there are genetic correlations between traits which means that evolutionary factors would have to effect all of the traits rather than a single one (Hecht et al 2015), and 2) that some regions of the genome appear to be associated with multiple migratory related phenotypic traits. However, as mentioned above concerning the inversion on chromosome 5, the same phenotype in different populations appears to not always be caused by the same genetic variations and chromosomes 12 and 14 are not always important in the development of migratory related traits. Rainbow trout are a good non-model species to study the genetic basis of migration because 1) they often have both life-history types in the same river (Hale et al 2013), 2) and have a plethora of individual level phenotypic data (Wapels et al 2019), and 3) there is a complete genome sequence.

A large part in understanding Salmonid genomics is looking into SNP data and seeing how those data are associated with important phenotypic traits. For example, based on SNPs in a 140-kb region on chromosome 28 in Chinook Salmon it can be determined if a fish is a spring or fall run

and in a 30-kb region it can be determined by the SNPs if a fish is a spring and winter run (Harringmeyer et al 2020). Like the examples above, this emphasizes the genetic basis of migration and therefore that not only migration can be inherited, but also whether a fish returns in spring or fall from its ocean migration is also inherited. In addition, SNPs can be assessed in genome wide association studies. This was used by Hu to look at SNPs associated with migration in rainbow and steelhead trout. It was found that there were 504 highly heritable SNPs associated with migration in two populations, one that had access to the ocean and one that did not (Hu et al 2014). Since heritability is high that indicated that there is some amount of genetic control of migration. Using population genomics, Hale was able to determine specific loci that have specific differences between migratory and non-migratory populations. The three genes that had significant SNPs in Hale's study were Gonadotropin subunit beta-2 (Gthb2), SOX14, and sperm-associated antigen 16. All of these are important for mating. Gthb2 is important in regulating the return timing for spawning chum salmon. In addition, Waples also found significant SNPs on loci Greb11 in Chinook and Steelhead that also directs the timing of adult spawning migration, in addition to genes on chromosome 9 that are linked with sexual maturity and run timing. Greb11 is responsible for the estrogen-responsive gene (Harringmeyer et al 2020). The homologous region of Chromosome 9 for Pacific Salmon is correlated with spawning ecotypes (Wapels et al 2019). SOX14 is important in *O. mykiss* for sexual differentiation (Hale et al 2013). Since we know that timing sexual maturation effects if a salmon will migrate or not as smolification delays sexual maturity, changes in expression of these genes will have an effect on migratory behaviors.

Previous research on understanding the genetic basis of migration in rainbow trout suggests that while it is clear that genetics plays a significant effect, there are different regions of the genome

associated with migration in different populations. Therefore, although different fish in different populations are exposed to similar environmental cues – such as increases in day length and temperature - populations with different alleles can still produce both migrant and resident phenotypes (Weinstein et al 2019). Thus, suggesting some level of population specific genetic effects. Although this certainly suggests the genetic control of migration in rainbow trout is complex, it also means conservation efforts to preserve endangered and threatened migratory populations require a thorough understanding of the alleles associated with migration on a population specific level.

Conclusion:

Genomics can help our understanding of the genetic control of migration. These data will allow us to understand more fully what genes and alleles allow an individual to migrate or increase its chance of residency. Specifically in salmonid species we discussed how SNPs and chromosomal inversions can be crucial in predicting the life history of the individual. In order to fully understand migration in salmon more research in heritability, environment, and specific genes is required, ideally from multiple populations. For heritability, research regarding early life history transition for the wild populations of rainbow trout and steelhead trout would be advantageous because it will allow us to better conserve migratory populations. Although the focus of this paper is on genetics, the environment also plays a large role in how migration genes are expressed especially when it comes to dictating how individuals utilize resources. Another interesting observation is that the genomic control of migration varies based on the latitude of the population, so more in depth research about how latitude effects life histories and the expression of genes would provide more clarity. Lastly, olfaction is important for salmon to return home

after migration (Hale et al 2013). Observing and analyzing SNPs in olfaction genes could give us more insight to predictors of life history. This would allow us to have population specific control enabling conservation strategies that with genetic information from every threatened population of salmonid would be increasingly effective.

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