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IN FOCUS

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The phenology of migration in an unpredictable world

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Abstract

In Focus: Freshwater, C., Trudel, M., Beacham, T. D., Gauthier, S., Johnson, S. C., Neville, C. & Juanes, F. (2016) Individual variation, population-specific migration behaviours and stochastic processes shape marine migration phenologies. *Journal of Animal Ecology*, *88*, 67–78. https://doi.org/10.1111/1365-2656.12852

Pacific salmon undertake arduous and risky migrations from their freshwater nursery grounds to the coastal ocean, northwards to their feeding grounds, and then back to their freshwater natal habitats to spawn. Understanding the phenology of such migrations has largely been viewed through the lens of microevolution producing optimal strategies that reflect local selection pressures; less emphasis has been placed on quantifying how variation in migration patterns can spread the risks associated with life in variable and unpredictable ecosystems. In this issue, Freshwater et al. use the information contained in ear stones (otoliths) and DNA of migrating juvenile sockeye salmon from the Fraser River of western Canada to quantify variation in the timing of their marine migrations. Not only were there population-specific differences in migration phenology of fish from the same river, but there was substantial variation among individuals from specific populations. These patterns also varied from year to year. Data like these emphasize the risks involved in such migrations and suggest that variation in key migration traits are maintained because of the inherent unpredictability of ecosystems. Management and conservation efforts would be well-served to consider actions that maintain such ecological variation to facilitate meta-population persistence in a rapidly changing world.

KEYWORDS
bet-hedging, match-mismatch, phenological variation, salmon, smolt

The long-distance migrations performed by many species are among the most spectacular phenomena in nature. Over the course of completing their life cycles, many organisms walk, fly or swim thousands of kilometres to move among ecosystems that offer alternative growth, survival and breeding opportunities. These migrations are impressive from the standpoint of the distances over which animals move and often by the sheer size of the aggregations of individuals involved. Less appreciated is that many of these individuals embark on migrations without ever having done so before and often without the benefit of older conspecifics who might help them navigate successfully. While individuals may not have previously performed such migrations, their genes have, providing them with a developmental programme selected through generations of successful ancestral trips that should offer them some hope for successfully completing their own life cycle.

A primary challenge for long-distance migrators is that they are usually on a trip where they cannot know what the conditions are at their destination and there is little opportunity to turn back if they encounter poor conditions on the way. The seasonal timing (phenology) of migrations is often critical for determining the conditions experienced during migration in seasonally variable environments (Figure 1). Sockeye salmon (*Oncorhynchus nerka*) spawning in the Fraser River of British Columbia (Canada) migrate to the ocean after spending a year growing in lakes, often hundreds of kilometres

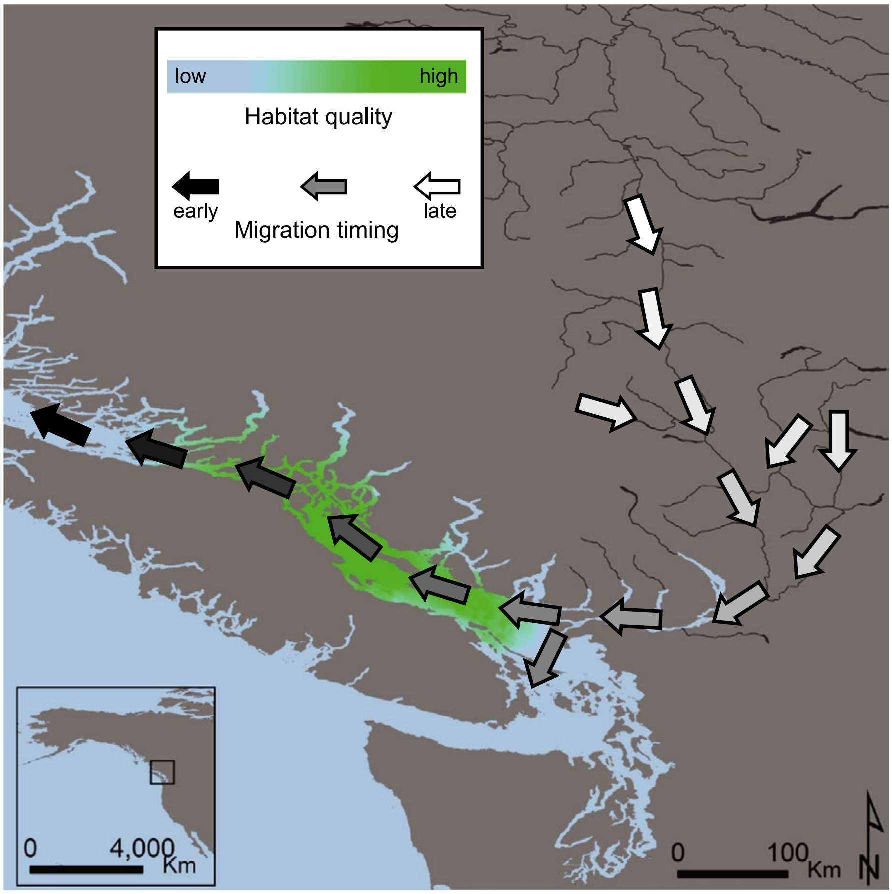

FIGURE 1 Hypothetical illustration of how the phenology of oceanward migration by juvenile salmon affects the quality of habitat they encounter in the coastal ocean. The intensity of green is intended to show the highest quality habitat, but one that is temporally ephemeral due to seasonality in plankton dynamics, predators, water temperatures and other environmental conditions. Arrows are intended to show the locations of juvenile salmon at a distinct point in time, but that have different migration timings. In this example, fish that migrate early from the river have moved northward before the best habitat conditions have developed. Fish that migrate late might miss capitalizing on the best quality habitat by the time they arrive in the ocean. Individuals with intermediate migration timing happened to migrate through the best habitat conditions in this example. We should expect the spatial and temporal dynamics of coastal habitat conditions change markedly among years, thereby maintaining variation in oceanward migration timing by juvenile salmon

from the ocean, and then swim north along the coast to the Gulf of Alaska to feed and grow before initiating their return migration to their natal river to spawn. Environmental conditions, including water temperatures, the state of plankton communities on which they feed, and the abundance and distribution of their predators, vary considerably across space and time, and from year to year in the coastal ocean. Thus, when juvenile sockeye salmon embark on their migrations to marine feeding areas, they do so facing innumerable uncertainties ahead. How do they succeed? What are the attributes of the juvenile migration strategies for populations that have persisted for millennia?

Freshwater et al. (2018) accomplished an ambitious study to quantify the phenology of the oceanward migrations of juvenile sockeye salmon from the Fraser River. Given the immense size of this river, it is impossible to tag enough juvenile salmon that you could recapture them at a later date to determine how their migration timing and growth patterns were related. Instead, Freshwater et al. (2018) used two natural markers in juvenile sockeye salmon caught in the coastal ocean to determine their natal origins in the vast Fraser River watershed and also to quantify the timing of their migrations to the ocean. Specifically, they sampled otoliths (ear stones) whose microstructure can be used to infer body size, growth rates and the timing of habitat transitions throughout a fish's life. Genetic information in DNA (microsatellites) was used to assign individuals to their population of origin from among nine distinct populations distributed across the Fraser River basin. Together, these two sources of information could be used to determine the date at which a fish entered the ocean from the river and whether the natal origin of that fish had any effect on its phenology and other migration behaviours.

The key insight that emerged from this study was that there is not a single migration pattern that characterizes juvenile sockeye salmon from the Fraser River. Freshwater et al. (2018) quantified substantial variation among years, stocks and individuals, in terms of their migration phenology, growth trajectories and the duration of their residency in the coastal ocean. Juvenile sockeye salmon that survived their first month at sea entered the ocean over a relatively broad window of time (up to 50 days), and the timing of this window varied among years. Further, there were modest differences in the timing of when smolts from different stocks entered the ocean to initiate their migration to the Gulf of Alaska. In addition to substantial variation in the timing of their entry to the ocean, individuals also showed marked variation in the length of time they took to migrate from the mouth of the river northwards along the coast. Fish that grew slowly tended to take longer to migrate than those that achieved high growth rates.

This work emphasizes an emerging theme in migration ecology that variation in timing is likely a characteristic of persistent populations and meta-populations. Ecologists have tended to emphasize the coordinated nature of large-scale migrations, which suggests the importance of evolution producing strategies for matching optimal conditions for growth and survival, and for tactics such as swamping predators. However, the results of Freshwater et al. (2019) and others (e.g., Carr-Harris et al., 2018; McGlauflin et al., 2011; Scheuerell, Zabel, & Sandford, 2009) highlight the fact that there is substantial variation in these biological traits both within and among populations. Evolution may produce more bet-hedging in migration strategies than has been emphasized in ecology in general (Schindler, Armstrong, & Reed, 2015) or has been emphasized in the conventional wisdom of salmon ecology that tends to focus on the microevolution of local optima (Quinn, 2005).

Variation in migration timing and duration has important implications for the population dynamics of migrating species and for other species with which they interact. For a migratory species, variation in migration phenology likely spreads the risks associated with moving between habitats where the conditions that lie ahead are seasonally variable and unpredictable. Such variation in migration timing is likely to improve the chances that some individuals from a population, or some offspring from a given parent, will encounter favourable conditions for growth and survival (Figure 1). Such risk-spreading should stabilize population dynamics if migration between habitats represents a critical fitness bottleneck, as it typically does. Second, for the predators that often aggregate to feed on the dense aggregations of migrating organisms, variation in migration timing likely prolongs the season over which they can capitalize on the high-quality feeding opportunities provided by migrating prey. Thus, phenological variation likely enhances some resource flows to top predators (Armstrong, Takimoto, Schindler, Hayes, & Kaufman, 2016).

Understanding of the ecological and evolutionary processes that generate and maintain variation in migration phenology within and among populations will likely emerge with renewed research interest in this topic and new approaches for quantifying variation such as those used by Freshwater et al. (2018). However, the implications for management and conservation should already be clear. Given that migratory animals such as sockeye salmon live in a world with substantial variability and unpredictability, management and conservation efforts should strive to maintain the habitat and genetic diversity that maintains variation in key life history traits (Schindler et al., 2008). This variation in life history traits, their genetic basis and heterogeneous habitat conditions will provide options for organisms to persist and thrive in a constantly changing world.

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