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Climate-driven straying dynamics in anadromous salmon and steelhead: Research agenda for conservation

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Anadromous salmonids of the genera *Oncorhynchus*, *Salmo* and *Salvelinus* (hereafter, 'salmon'), are culturally, economically and ecologically important fishes, affected by climate change at every life stage. Predictions about their future distribution and abundance are typically based on thresholds of thermal tolerance and changes to phenology in response to warming rivers, shifting flow regimes and complex marine processes (Crozier & Siegel, 2023). Numerous conservation efforts focus on mitigating climate change, mainly in spawning and rearing habitats via restoration efforts to increase population resilience and capacity. While habitat alterations may dominate the narrative for salmon in a climate-altered future, indirect effects of climate change will likely be nuanced and in combination with other human activities. One such process involves the straying of natural- ('wild') and hatchery-origin salmon through climate-driven changes in olfactory imprinting and detection of olfactory signals, and trade-offs between homing and spawning habitat selection (Figure 1).

The great majority of surviving salmon return from the ocean to natal spawning grounds, guided by olfaction and other sensory inputs. Homing isolates spawning populations, favouring local adaptation (Dittman & Quinn, 1996). Straying (spawning in non-natal sites) is also a natural phenomenon that may reflect a failure to locate the home river or a rejection of the natal site. While the terms homing and straying suggest binary alternatives, there are nuances. For example, straying can include fish spawning in a non-natal river, fish entering their natal river but spawning in a non-natal tributary, or hatchery-origin fish returning to their natal river and spawning there rather than entering their hatchery (Pollock et al., 2020). Whether a fish is considered to have strayed depends on the spatial scale of observation, with lower stray rates observed at larger geographic areas (e.g., basin) and higher stray rates at smaller areas of study (e.g., tributaries); this discrepancy is more pronounced in hatchery salmon that stray at higher rates at local scales (Pearsons & O'Connor, 2024). Stray hatchery-origin salmon are especially problematic for fisheries managers attempting to limit genetic and ecological impacts on wild salmon (Keefer & Caudill, 2014).

Homing to natal rivers necessitates fish imprinting upon stream-specific chemical signals at one or more early life stages, retaining the memory without reinforcement while they feed in distant waters, and initiating upstream migration when they detect these signals in rivers as maturing adults. The sequential imprinting hypothesis (Keefer & Caudill, 2014) posits that juvenile salmon learn a series of olfactory waypoints, beginning at the natal site as they migrate towards the sea, and then use these waypoints to retrace their path as returning adults. To return home, adult salmon likely rely on a sequence of signals, including geomagnetic information at sea, transitioning in rivers to and imprinted odours, followed by conspecific cues, and then non-olfactory environmental inputs such as temperature and substrate (Bett & Hinch, 2016).

The complex process of imprinting and homing in wild and hatchery-origin salmon may be further complicated by climate

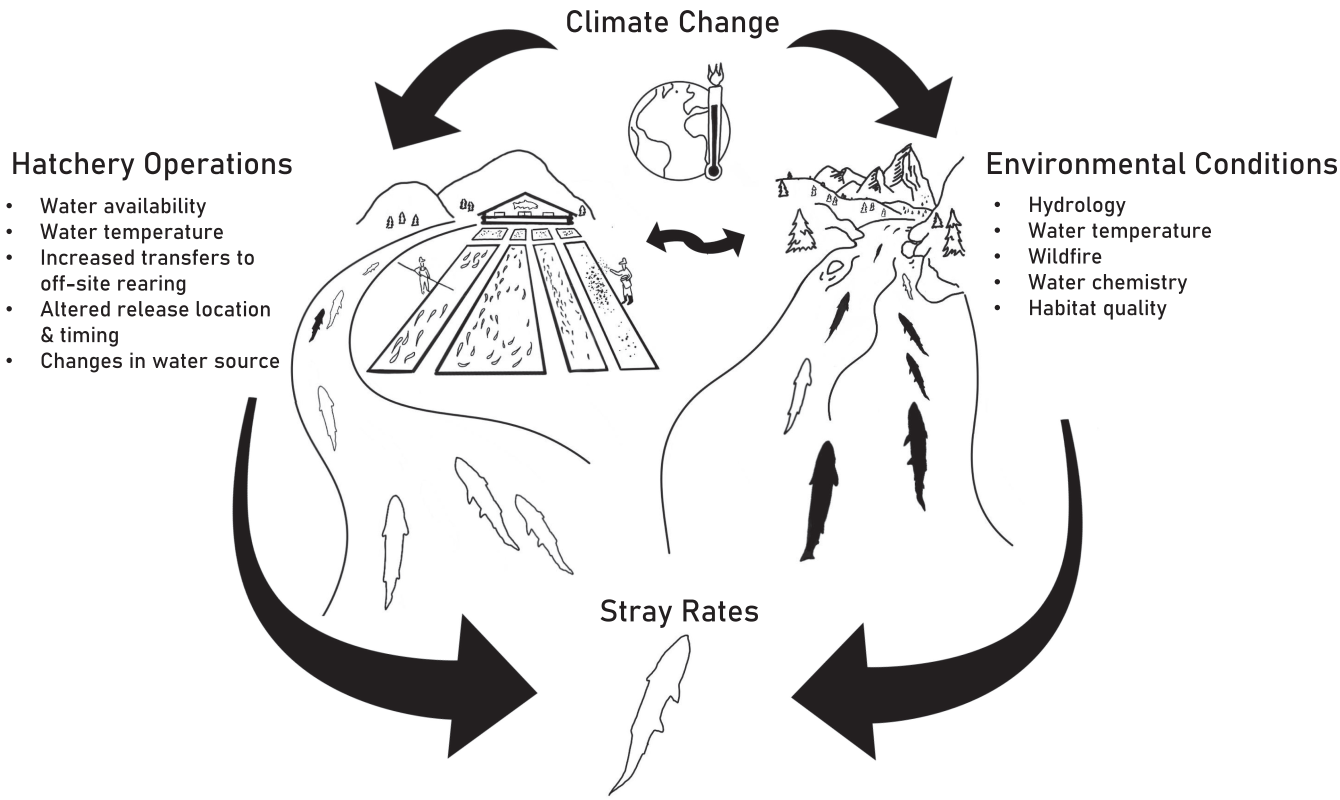

FIGURE 1 Conceptual diagram indicating impacts of climate change on environmental conditions and hatchery operations, each in turn affecting stray rates (direction of arrows indicates direction of effect). The bidirectional arrow acknowledges environmental conditions will affect hatchery operations and vice versa. Straying creates exchange between wild (black) and hatchery (white) spawners.

change (Bett et al., 2017; Bett & Hinch, 2016). For example, increasing river temperatures experienced during spawning migration can spur fish to enter cool, non-natal tributaries (Bond et al., 2017; Keefer et al., 2018). They then may exhibit straying or high homing fidelity after using thermal refugia in non-migratory habitats, depending on the species (Pearsons & O'Connor, 2020). If salmon spawn in non-natal tributaries rather than resuming migration, this constitutes straying and not mere behavioural thermoregulation (Keefer et al., 2018). Temperatures in the Columbia River and its tributaries were positively correlated with straying (Westley et al., 2015), likely reflecting a behavioural conflict between homing and thermoregulation and would presumably affect natural- and hatchery-origin salmon alike. In many rivers, climate models predict higher temperatures and lower flows in late summer and fall (Crozier & Siegel, 2023). In these cases, natal rivers might be recognised as home but perceived by salmon as unsuitable for spawning. Climate-related factors beyond temperature such as ocean acidification and increased oceanic CO_2 could inhibit salmon olfaction in a way that carries into their freshwater migration (Bett & Hinch, 2016).

Hatcheries are subject to many of the climate change impacts that affect riverine systems, but effects are also likely to involve management responses to environmental challenges. A review of climate impacts on National Fish Hatcheries in the US Pacific Northwest listed increasing air temperature, altered rainfall and hydrological cycles in rivers, and seawater intrusion as possible effects of climate change (Hanson & Ostrand, 2011). Changes to water sources at hatcheries with different chemistries (e.g., increased reliance of groundwater vs. surface water) could affect imprinting and homing (Harbicht et al., 2020). One management response to climate change is to increase the transport of juvenile hatchery-origin salmon to rearing facilities with cold water or to release sites that reduce seaward migration distance. In response to increasing drought conditions in California's Central Valley, millions of hatchery salmon have been annually transported and released downstream, drastically increasing stray rates from <10% to as much as 89% (Sturrock et al., 2019). In another example, hatchery- and natural-origin steelhead *O. mykiss* (Walbaum, 1792) that had been barged down the Snake River as juveniles were 73 times more likely to enter a non-natal tributary as adults (where no hatchery programme exists) than fish allowed to complete their natural downstream migration (Tattam & Ruzycki, 2020). Hatchery-origin Chinook Salmon *O. tshawytscha* (Walbaum, 1792) transported by barge as juveniles from the Snake River and released below the confluence with the Columbia River also had higher adult stray rates than in-river migrants and juveniles permitted to migrate past the confluence before barging (Bond et al., 2017). Beyond release location, imprinting may be affected if climate-driven increases in water temperatures at hatcheries necessitate earlier release of smolts, generating a mismatch between photoperiod-linked smolting and imprinting opportunity (Sturrock et al., 2019).

Considering climate-driven changes to the natural environment and hatchery operations that may affect straying—itself an incompletely understood phenomenon—a dedicated research agenda is needed. We suggest research into the following topics will generate valuable insights and advance our understanding to improve salmon management and conservation:

Straying dynamics and mechanisms in salmon:

1. enhance understanding of wild fish stray rates to understand causes of straying and establish reference points for hatchery salmon;
2. explore the mechanisms governing olfactory imprinting and their genetic or epigenetic basis, including the development of physiological, neural and genetic proxies to help understand the timing and mechanisms of imprinting;
3. determine links between climate drivers (including water temperature, hydrology, wildfires, etc. and co-stressors such as anthropogenic pollutants) and straying variation among salmon life history types, populations and species; and
4. further evaluate how off-route juvenile rearing patterns influence homing and straying.

Hatchery practices and climate adaptation:

5. assess the effects on straying rates from transportation among hatcheries and use of release sites that climate change may necessitate;
6. increase understanding of how changes to salmon release timing and location affect straying;
7. evaluate how altered water sources in hatcheries (e.g., using groundwater vs. river water; recirculated water) affect imprinting and straying; and
8. explore cost-effective approaches to manipulate odours that can improve homing of hatchery salmon to adult collection facilities and acclimation sites, including evaluation of the spatial scale of effective olfactory cue manipulation.

Conservation and interdisciplinary collaboration:

9. establish long-term monitoring programmes to assess straying in hatchery and especially wild populations (e.g., with PIT tags—see Pearsons & O'Connor, 2020; or other marking technologies);
10. measure demographic and genetic impacts of straying on donor and recipient populations and integrate with models of climate effects; and
11. promote interdisciplinary collaborations and knowledge-sharing among researchers, managers and stakeholders to address the above research agenda, emphasising exchanges between scientists and practitioners in different regions and nations, working on different species.

In summary, we urge researchers and managers to consider the indirect effects of straying dynamics on the distribution and abundance of anadromous salmon and steelhead in a climate-altered future. The interplay between environmental factors, hatchery operations and the complex nature of straying requires attention through a dedicated research agenda. The proposed agenda is intended to serve as a roadmap for advancing our understanding and informing effective conservation strategies for culturally, economically and ecologically important salmon in the face of a rapidly warming climate.

AUTHOR CONTRIBUTIONS

All co-authors contributed to the ideas underlying and the writing of this article.

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