

Juvenile salmon non-natal rearing via habitat shifting through the marine environment

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Executive Summary

Salmon exemplify numerous life history strategies as they transition between freshwater and marine environment during their complex life cycles. Importantly, this life history diversity varies among species and populations and is well understood to provide resilience. Yet such complexity has also left some salmon particularly vulnerable to habitat degradation and loss, precipitating substantial population declines. Among the myriad management actions underway, protecting and restoring juvenile rearing habitat have been identified as critical to salmon recovery. Much of that effort has focused on juvenile rearing habitat *within* natal watersheds (i.e., the watersheds where salmon spawn and emerge). This is appropriately due to the assumption that juvenile salmon primarily rear in their natal watersheds before dispersing to mature in the ocean. However, observations over the past two decades have revealed that juvenile salmon will also successfully rear in non-natal habitats. Much research has focused on non-natal habitat rearing in non-natal tributaries or non-natal areas downstream of spawning grounds. These types of non-natal habitats are often still within the natal watershed. However, there are also examples where juvenile salmon disperse out of their natal watershed, enter the marine environment, and re-enter freshwater or brackish habitats, including in non-natal estuaries or streams to rear. This behavior, which we term ‘habitat shifting through the marine environment’ (HSME), is largely absent from dominant conservation discussions for salmon populations. Here, we review the evidence for HSME across salmon species and geographies. We found that HSME has been widely observed throughout the Puget Sound region, particularly in the Whidbey Basin but also in Central Puget Sound (King and Kitsap Counties) and Hood Canal (Mason and Jefferson Counties). Beyond Puget Sound, we found evidence for HSME throughout the Pacific from Alaska to California and Japan. There was also evidence for HSME in Baltic Sea salmonids. The evidence for HSME was dominated by Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*), likely due to disproportionate research in Puget Sound and the eastern Pacific more broadly. But we also found evidence for HSME in chum salmon (*O. keta*), pink salmon (*Oncorhynchus gorbuscha*), masu salmon (*O. masou*), Atlantic salmon (*Salmo salar*), and brown trout (*S. trutta*). Most HSME was observed in smaller coastal streams but there is also important evidence for HSME into barrier embayments (e.g., pocket estuaries) and into non-natal large river deltas. The evidence for HSME is more expansive across species and geographies than is perhaps generally recognized. The relatively widespread nature of HSME underscores the importance of not discounting small systems without salmon spawning as fishless habitats. Recognizing the commonness of HSME may afford new opportunities for protective and restorative measures in habitats like smaller coastal streams that have seldom been prioritized for salmon recovery. Such actions may be particularly important given the century-plus legacy of impacts that have potentially limited access for juvenile salmon to these habitats. Importantly, as individual fish travel farther from natal watersheds or over longer periods of time, the need for non-natal habitat likely diminishes as fish grow larger and become further acclimated to marine environments. Finally, the conservation community may have experienced a “shifted baseline” for what constitutes normal salmon habitat use given some of the most intensive impacts to these atypical rearing habitats occurred decades before salmon declines were considered critical. Including non-natal habitats in restoration and recovery plans is likely valuable and could benefit from a framework that considers the spatial arrangement (relative to natal sources) and condition of habitats as well as desired current and future population abundances. Such a framework would rely on increased coordination among recovery jurisdictions as benefits of non-natal habitat use will often transcend population and jurisdictional boundaries.

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Introduction

Salmon (*Oncorhynchus* spp. and *Salmo* spp.) are one of the most culturally-, economically-, and ecologically-valuable group of species. Recent decades have witnessed substantial declines in salmon stocks, including multiple salmon species and population segments of Chinook (*O. tshawytscha*), coho (*O. kisutch*), and chum (*O. keta*) in the western United States. These declines have impacted cultural resources, resulted in a loss of harvest opportunities, and influenced broader biotic communities including killer whales (*Orcinus orca*). As such, there has been considerable investments in habitat protection and restoration efforts such as improving adult spawner passage, juvenile rearing habitat extent, riparian protections and plantings. The slow or limited recovery of salmon stocks to date underscores the need to understand additional habitat elements that may be limiting populations.

Salmon rely on several habitat types throughout their life cycle as they migrate between freshwater and marine environments. Timing of migration, residence time, habitat sequencing, and repeated use or spawning (iteroparity) within particular habitats can all vary with species and life history strategy (Quinn 2005, Groot and Margolis 1991). Maintaining variability in such traits and the habitats that support them is critical for supporting species and population resilience (Schindler et al. 2010, Greene et al. 2010, Bourret et al. 2016).

Habitat conditions also play a role in determining how individuals distribute, behave, and perform in particular locations throughout their life cycle (Sturrock et al. 2020, Beechie et al. 2006). Habitat loss and degradation over the last century-plus has had an impact on multiple species and life stages resulting in population declines across their range (Finn et al. 2021, Zeug et al. 2011). Recovery efforts for impacted populations have reasonably focused on restoring habitats within natal watersheds (i.e., watersheds where salmon reproduce) to benefit both spawning and rearing conditions with goals to improve population productivity and abundance (National Oceanic and Atmospheric Administration 2017).

However, observations of juvenile salmon rearing in habitats *outside* their natal watershed has raised general questions about the ecological role these habitats may play in promoting resilience and, more recently, population recovery (Beamer et al. 2003, Koski 2009). For nearly two decades, there has been uncertainty around the use of non-natal embayments and small coastal streams by multiple salmonid species and the relevance of these habitats to salmon recovery (Redman et al. 2005). Documenting the use, extent, and diversity of non-natal habitat use outside of the natal watershed may be critical for adapting current recovery plans and restoration prioritization, especially given changing climate conditions and potential impacts on depressed species and/ or populations (Cordoleani et al. 2021). In 2022, as part of the project “*Science Sprints to Support Regulation*” funded by the Puget Sound Partnership, regulators from the National Oceanic and Atmospheric Administration (NOAA) and Washington Department of Fish and Wildlife (WDFW) – in consultation with other regional regulators – identified juvenile salmon rearing outside their natal watersheds as a biological phenomenon that would benefit from a science synthesis to inform regulatory actions and local restoration priorities.

Our goal here is to synthesize available information and describe the phenomenon of non-natal habitat use by juvenile salmonids. While we emphasize the relevance to Puget Sound salmon recovery, we synthesize relevant information for salmonids across geographies and present a generalized description of this behavior for this group of fishes.

What is non-natal habitat use?

Salmonids may demonstrate non-natal habitat use during spawning and rearing life stages. Non-natal habitat, as it pertains to salmonids, may be classified into use by two primary life stages: spawning and

rearing. Non-natal *spawning* habitat use, generally referred to as “straying”, occurs when mature adults return to spawn in a river or tributary different from that which they emerged (Quinn 1984). A large body of research exists exploring the rates of straying (Ford et al. 2015, Keefer and Caudill 2014), factors that influence straying (Sturrock et al. 2019, Bond et al. 2017, Westley et al. 2013), the evolutionary causes and consequences of straying, and differences in straying among species or populations (Westley et al. 2013). In contrast, non-natal *rearing* habitat use during juvenile life stages has received considerably less attention, although observations of this behavior have existed for decades (Healey 1991). Rearing, in this case, refers to behaviors or habitats that support growth or physiological development at early life stages.

Non-natal *rearing* habitat use is nuanced and depends primarily on the scale at which natal habitat is defined. Numerous studies have documented individual movements between freshwater tributaries *within* a natal watershed (Murray and Rosenau 1989, Miller and Sadro 2003, Tabor et al. 2011, Bourret et al. 2016, Phillis et al. 2018). While these observations demonstrate movement out of a natal reach or tributary, the juvenile fish remain within a natal watershed. In this case we define a natal watershed as any freshwater or estuarine habitat that is accessible to individuals from emergence without entering the marine environment. A natal watershed could include several tributary watersheds that together terminate in a single estuarine feature that joins the marine environment. Movements among habitats within the natal watershed thus follow the typically-understood salmon migration sequence along a salinity gradient (**Figure 1**). Such behavior may also occur between freshwater and estuarine habitats within watershed (Koski 2009). Evidence suggests that access to and opportunity provided by these alternative habitats supports life history diversity and may be critical for maintaining population resilience given a warming climate (Munsch et al. 2019, Munsch et al. 2020). Most research on non-natal habitat use to-date has emphasized non-natal habitat *within* the natal watershed, such as non-natal tributaries of a natal river.

Non-natal rearing or habitat use can also occur when juveniles migrate outside of their natal freshwater environment, *through* marine waters, and enter additional freshwater or estuarine habitats during early life stages (Beamer et al. 2003, Koski 2009, Beamer et al. 2013; **Figure 1**). Put another way, this form of non-natal habitat use differs from the conventional linear habitat transitions along the salinity gradient from fresh to saltier water via movement back into less saline water for rearing. As such, this behavior requires an individual to entirely depart natal watersheds, including past non-natal reaches and tributaries within a natal watershed, into nearshore marine waters prior to finding suitable freshwater or estuarine environments to rear in that are in alternative, non-natal watersheds. Presumably, individuals then resume use of these alternative habitats in the typical natal strategy/sequence. However, the duration and residence within these non-natal habitats remains minimally studied. Researchers in the Baltic Sea have termed this behavior ‘stream shifting through the marine environment’ (SSME) after observing juveniles of both *S. trutta* and *S. salar* rearing in streams outside their natal watersheds, indicating that juvenile fish left their natal watershed, entered the marine environment, and continued rearing in alternative freshwater or estuarine habitats (Taal et al. 2017, 2018).

Here we extend Taal et al.’s SSME definition to include estuarine or brackish environments in addition to freshwater streams. We therefore adapt the term SSME to ‘*habitat shifting through the marine environment*’ (HSME) to reflect the variety of freshwater and estuarine habitats that are included in our conceptual model of non-natal habitat use.

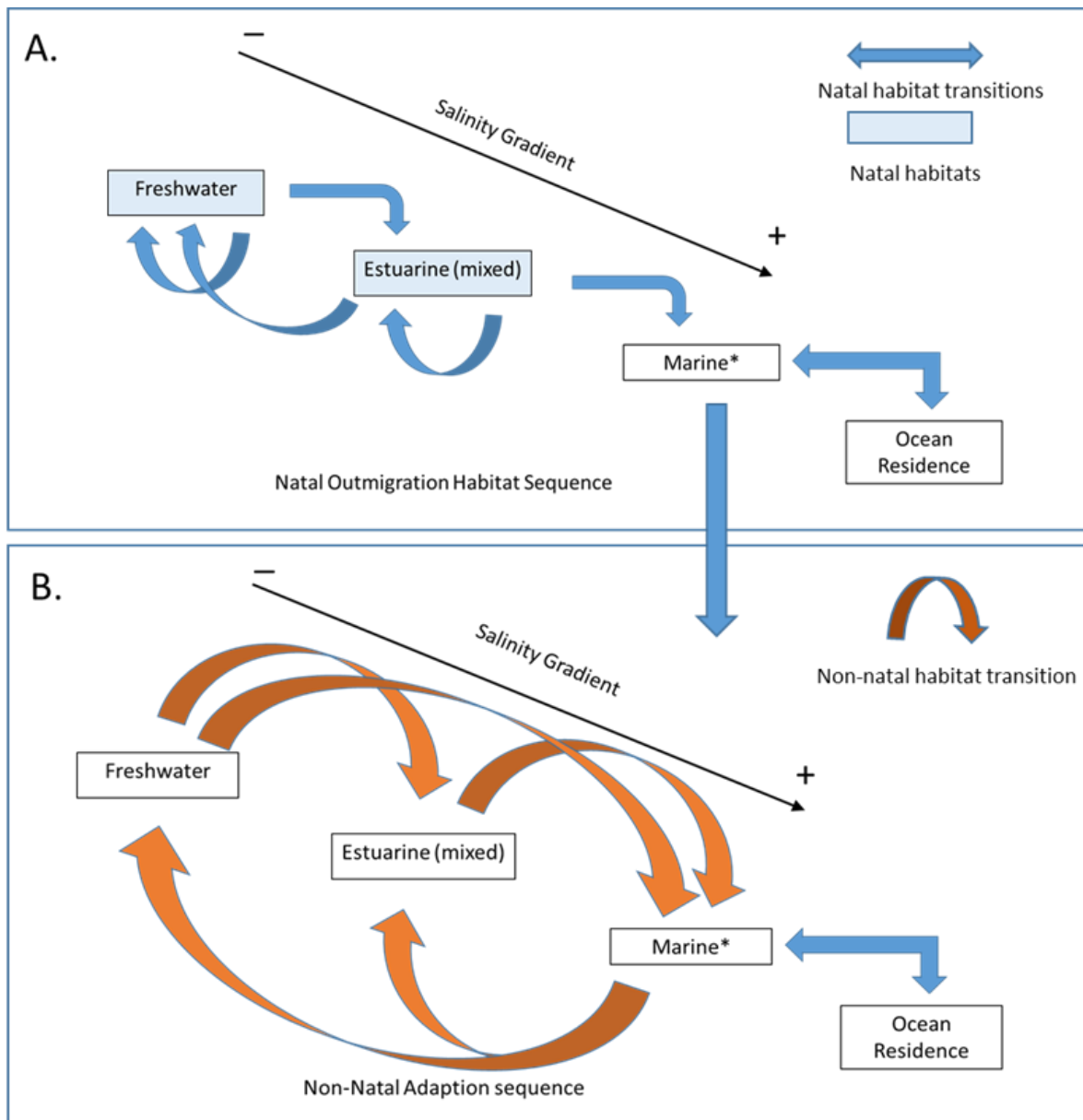


Figure 1. Conceptual diagram of non-natal habitat use by juvenile salmon. A) typical habitat sequence for outmigrating juvenile salmon along an increasing salinity gradient and B) non-natal habitat sequence by which juveniles re-enter fresh or brackish habitats after migrating through marine waters. *For our purposes, marine habitats are indicative of other, non-brackish, shoreline features.

Habitat classes included in HSME

HSME is not defined, necessarily, by a specific habitat type or feature but rather a deviation or adaptation in the sequencing of habitats along the salinity gradient. Individuals exhibiting non-natal strategies will alter the sequence via the use of alternative freshwater or estuarine habitats subsequent to initial marine exposure. Yet, properly classifying or identifying potential non-natal habitats under our definition of HSME is critical for documenting the phenomenon. Accurately classifying HSME is also essential for potentially including and prioritizing these habitats in protective policies, recovery plans, and restoration

programs. We propose a habitat classification into three primary features which encompass a range of specific habitat types and which are largely informed by local geomorphic characteristics and processes (**Figure 2**; see Collins and Shiekh 2005).

For any of the habitat features discussed below to be considered ‘non-natal’ there can be no documented observations of anadromous spawning activity for a particular focal population of a given species. This can include systems where a species is already spawning but juveniles of another population of the species use that habitat for rearing but not spawning. For our purposes, we include the following habitats classes in our current synthesis, each defined in more detail below: 1) river deltas, 2) embayments, and 3) small coastal streams (**Figure 2**). Under our definition of HSME, we exclude strictly marine shoreline features that primarily reflect habitats used by juvenile salmonid along their seaward migration pathway (**Figure 1A**). However, we acknowledge that these features, and in general nearshore environments adjacent to natal rivers, are important rearing habitats for juvenile salmon during early life stages (Beamer and Fresh 2012, Marin Jarrin et al. 2016, Pucci et al. 2017).

River deltas are features formed at the mouth of generally large river systems where freshwater meets the marine environment. The river delta class can be characterized by hydrology patterns representative of mountainous headwaters and large freshwater influx (Collins and Sheikh 2005). These features are commonly composed of several components including a delta fan, distributary and tidal channels, and a marsh plain distributed across a range of elevations influencing the tidal prism across the delta. Large river deltas may act as natal habitat for salmon that spawn within the river system as well as non-natal habitat for juvenile salmon immigrating from other systems.

Embayments are a diverse class of features that differ based on geomorphology and post-glacial histories that influenced their formation (Collins and Sheikh 2005, Shipman 2008, McBride et al. 2009). Further, embayment features can be subdivided or categorized based on fluvial (sediment, freshwater) and marine inputs as well as the extent and type of any present barrier beaches. Examples of embayment categories included: drowned incised stream valley, drowned glacial topography, and embayments within bedrock and along rocky coasts.

Small coastal streams are characterized by two primary conditions: 1) no evidence for spawning for species or populations of interest and 2) emptying directly into marine waters with no detectable delta transition. Instead, the mouth of the stream and the lower stream itself flow through the beach and become inundated at the upper range of the tide series, although intertidal streams impacted by undersized crossings may have different features. Intertidal streams, under our current definition, are typically smaller and drain a watershed considerably less expansive than that of a large river. We note that this habitat type could benefit from a more robust definition with respect to size that is not simply relative to local, large river systems.

Methods

Between 24-27 February 2023 we used the program *Publish or Perish* to query Google Scholar for all references containing the phrases “salmon non-natal habitat”, “salmon non-natal coastal stream”, “salmon non-natal pocket estuary”, and “salmon non-natal tidal”. We collated the entries with the top 35 Google Scholar relevancy ranks from each search and removed duplicate references. We supplemented this systematic literature search by obtaining relevant studies (primarily from the gray literature) that we encountered elsewhere, including through consultation with regional and topical practitioners and researchers.

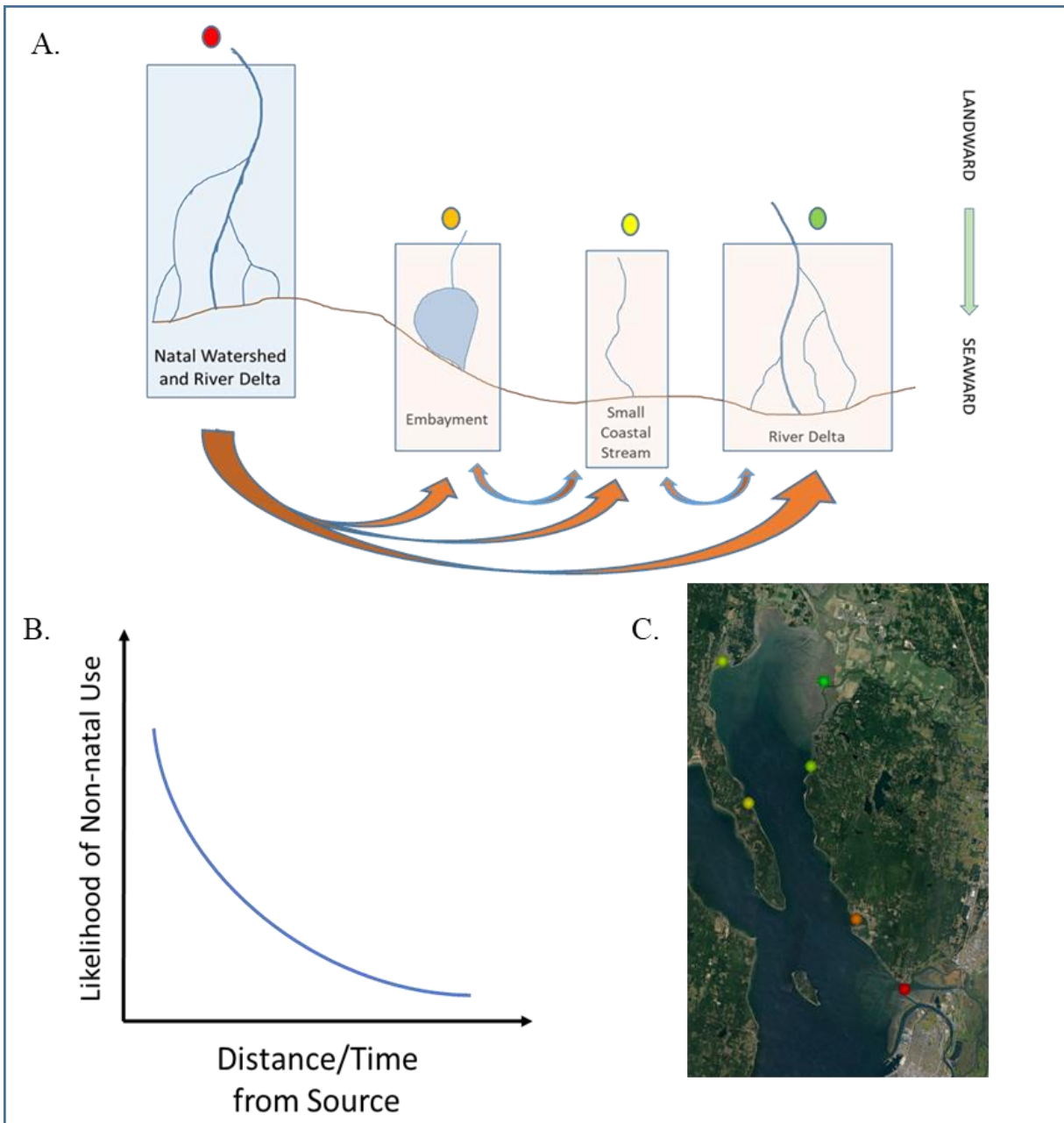


Figure 2. An A) illustration of habitat classes that provide opportunities for HSME in addition to B) the theoretical relationship between distance/time from source habitats and the likelihood of use as non-natal habitat and C) a conceptual example of the spatial arrangement of habitat classes/features and the likelihood of use for individuals exhibiting HSME. Colored dots in C correspond with those in A. Embayments represent several habitat types including those without freshwater input (see Collins and Shiekh 2005 for classification).

Revised Code of Washington (RCW) 34.05.271 requires WDFW to categorize sources of information used to inform technical documents that directly support the implementation of a state rule or statute. Because our review may be referenced in regulations [e.g., under Washington Administrative Code

(WAC) 220-660], we classify all references in the literature cited section into the following RCW 34.05.271 categories:

- (i) Independent peer review: Review is overseen by an independent third party;
- (ii) Internal peer review: Review by staff internal to the department of fish and wildlife;
- (iii) External peer review: Review by persons that are external to and selected by the department of fish and wildlife;
- (iv) Open review: Documented open public review process that is not limited to invited organizations or individuals;
- (v) Legal and policy document: Documents related to the legal framework for the significant agency action including but not limited to: (A) Federal and state statutes; (B) Court and hearings board decisions; (C) Federal and state administrative rules and regulations; and D) Policy and regulatory documents adopted by local governments;
- (vi) Data from primary research, monitoring activities, or other sources, but that has not been incorporated as part of documents reviewed under the processes described in (i), (ii), (iii), and (iv) of this subsection;
- (vii) Records of the best professional judgment of department of fish and wildlife employees or other individuals; or
- (viii) Other: Sources of information that do not fit into categories i - vii.

Results

The *Publish or Perish* Google Scholar searches yielded its maximum 1,000 results for the “salmon non-natal habitat” and “salmon non-natal coastal stream” queries, 154 results for the “salmon non-natal pocket estuary” query, and 475 results for the “salmon non-natal tidal”. After merging the top 35 Google Scholar results from each query, removing duplicate entries, and supplementing our formal review with additional literature provided by regional or topical experts, we obtained 23 references pertinent to out-of-watershed non-natal habitat use by juvenile salmon. Of these 23 references, 14 were gray literature (technical reports and theses) and the remaining nine were published in scientific journals. Most of the references produced from this search were either related to (1) non-natal habitat use by straying adult salmon or (2) non-natal tributary use within the natal watershed by juvenile salmon. Our search also yielded substantial gray literature that referenced relevant citations about HSME but which provided no new information on the phenomenon. We used these additional references to contextualize HSME within the broader theme of non-natal habitat use in salmon. Below we synthesize the findings from this body of literature based on geography, species and life history variation, and the three dominant habitat types used by salmon displaying HSME.

HSME by Geography, Species, and Life History

Our review indicated HSME was a generalizable salmon behavior that was not specific to a particular region or species. While observations were concentrated in particular geographies, documentation of HSME represented several different areas within the northern Pacific Ocean as well as the Baltic Sea. Evidence for HSME was concentrated within the northeast Pacific, particularly Puget Sound (e.g., Hirschi et al. 2003, Beamer et al. 2003, 2013, Bahls 2004, Kubo 2022, Tuohy et al. 2018) and included observations of non-natal habitat use from Alaska (see Koski 2009) to northern California (Wallace et al. 2015). However, there is also evidence for HSME in the northwestern Pacific as well, specifically Japan

(Kuroki et al. 2020). More recently, observations of HSME have also occurred in the Baltic Sea (there termed SSME; Taal et al. 2017, 2018) indicating the behavior may be widespread geographically, ecologically, and evolutionarily (e.g., Atlantic vs Pacific salmon).

There was considerable variation in observations for HSME among species, life history types, and origin (natural vs hatchery). Yet the breadth of observations among different species again indicates that HSME is not isolated to a single species although species-specific patterns may exist (described below). As evidenced in our regional description of HSME, most observations represented species of Pacific Salmon (*Oncorhynchus spp.*). However, the recorded observations of Atlantic salmon, although limited, included two species within the genus *Salmo*. Lastly, some convergence on specific life history types or migrant strategies exhibiting HSME appears evident in the literature across species and locations. Below we synthesize evidence for HSME by species and life history within each general region or geography.

Puget Sound

Most evidence for HSME is from studies within Puget Sound, WA. To our knowledge, the first documented cases of HSME in Puget Sound comes from the Whidbey Basin for Chinook (Beamer et al. 2003, 2013), a region within northern Puget Sound that contains three large river deltas and high proportions of extant natural salmon populations (National Oceanic and Atmospheric Administration 2017). HSME has been studied and monitored in Whidbey Basin consistently since the initial detection in the early 2000's. However, evidence for HSME extends beyond the Whidbey Basin to include much of the greater Puget Sound region including the Strait of Juan de Fuca and Hood Canal. Observations have been documented in all three HSME habitat types across Whidbey Basin as well as in several habitats within central Puget Sound (Glasgow and Jorgenson 2022, Kubo 2022) and Hood Canal (Hirschi et al. 2003, Bahls 2004, Tuohy et al. 2018). In addition, analysis of coded-wire tag data suggests non-natal habitat use may also occur in parts of South Puget Sound, adjacent to the Nisqually River delta (Hayes et al. 2019).

Four species of Pacific salmon (Chinook, coho, chum, and pink) were observed in non-natal habitat within Puget Sound. Chinook salmon were the most widely reported species exhibiting HSME behavior within Puget Sound (Beamer et al. 2003, 2013, Glasgow and Jorgenson 2022, Kubo 2022). Frequent occurrences of Chinook salmon have been documented in the Whidbey Basin while other synoptic observations have occurred in Hood Canal (Tuohy et al. 2018) and Central Puget Sound (Kubo 2022). Evidence from the San Juan Islands also suggests juveniles rearing in streams far from the nearest natal source (Beamer and Fresh 2012). Within Hood Canal populations, juvenile summer chum, pink, and Chinook salmon displayed HSME via use non-natal streams and barrier estuaries during their initial migrations (Hirschi et al. 2003, Bahls 2004, Tuohy et al. 2018). Pink salmon were also observed in relatively high densities, generally in even numbered outmigration years, in non-natal habitats within the Whidbey Basin (Kagley et al. 2007). Lastly, coho salmon were detected in several small non-natal streams across central Puget Sound using eDNA methods (Glasgow and Jorgenson 2022). While such techniques can indicate presence, they do not provide information on life stage, life history, or origin. HSME in coho was also documented for individuals migrating between two small streams in the western Strait of Juan de Fuca (Bennett et al. 2014). There is also at least one observation of an escaped hatchery coho juvenile (confirmed by a coded wire tag) rearing in a coastal stream on Camano Island (T. Zackey, *personal communication*).

Like observations in other geographies, the observations of HSME in Puget Sound have been largely representative of sub-yearling fish and specifically fry migrants (Bahls 2004, Beamer et al. 2003, 2013,

Tuohy et al. 2018, Kubo 2022). Nearly all observations of HSME for Chinook, pink, and chum salmon in Puget Sound were representative of fry migrant life history types or more generally individuals during their initial migrations soon after emergence. For pink and chum salmon this represents the primary/only life history strategy observed in Puget Sound. In contrast, Hayes et al. (2019) observed hatchery origin fish in the Nisqually Delta in south Puget Sound from as far away as central Puget Sound indicating the behavior is not exclusive to natural origin (i.e., wild) fish nor early migrants. Further, work on hatchery-origin juvenile Chinook in western Puget Sound found that juvenile fish can move dozens of kilometers from other streams within several days of release (Fresh et al. 2006). This suggests that juvenile Chinook can disperse quickly and over large distance and thus capitalize on non-natal habitats across large areas. Differences among populations with different adult return timing was also evident, specifically for fall- and summer-run chum salmon in Hood Canal (Tuohy et al. 2018). However, these differences were primarily evident in habitat preferences via HSME rather than in the behavior itself. Specifically, summer chum showed a stronger preference for barrier estuaries while fall chum showed an overall preference for small streams and delta channels.

Alaska and California

Observations of HSME within areas of the northeast Pacific outside Puget Sound have been limited but encompass the entire range of Pacific salmonids from California to Alaska. Koski (2009) reviewed observations and discussions around coho salmon juveniles, termed nomads, that migrate downstream as fry to estuaries to rear rather than stay in freshwater habitats. Koski (2009) describes a case study of Duck Creek in Alaska where coho juveniles reared in an estuary and then migrated to a non-natal stream to resume rearing. Conventional theory around coho salmon suggest these fish occur in estuaries because they are physically displaced by freshet high flows, because of intraspecific aggression, or due to limited rearing habitat. However, Koski (2009) argued that these nomads are not necessarily disadvantaged or neutral juveniles that are washed downstream or which are surplus. Rather, Koski (2009) suggested that these fish are taking advantage of quality downstream rearing habitat as an alternative life history or migratory strategy.

Additionally, mark-recapture efforts in Humboldt Bay, California found juvenile coho salmon inhabiting neighboring non-natal stream networks that could only be accessed by entering the marine environment and then re-entering the non-natal watershed (Wallace et al. 2015, Halloran 2020). The occurrence of HSME for coho within the Humboldt Bay streams was usually low (<1% of fish each year) and likely occurred during the second year as age-1 fish. Observations in Humboldt Bay were the only record we found of HSME occurring in fish after their first-year post-emergence.

Baltic Sea and Japan

To our knowledge, evidence of HSME in Atlantic salmon is relatively limited and recent. Taal et al. (2016, 2017) provide evidence based on otolith chemical signatures of individuals leaving their natal stream, migrating through marine waters, and re-entering freshwater environments in a non-natal watershed. The behavior was observed for both Atlantic Brown trout (*S. trutta*) and Atlantic salmon (*S. salar*) within coastal habitats of Estonia. In the case of *S. salar*, the fish moved from a non-natal stream into a larger river delta where *S. salar* spawn upstream. In contrast, some *S. trutta* moved into a non-natal small, coastal stream that was not suitable for spawning. Results suggest these movements occurred during their first year after emergence as individual fry (*S. trutta*, *S. salar*) and parr (*S. Salar*) migrants;

both of which represent notable observations of previously underappreciated and understood life history types for these species.

Similar observations of HSME have occurred within populations of masu salmon (*O. masou*) from northern Japan (Kuroki et al. 2020). Specifically, there is both capture-mark-recapture and otolith strontium:calcium ratios showing juvenile masu salmon enter brackish water and rear for some time before returning to freshwater to complete rearing. However, in some instances these juvenile masu salmon re-enter freshwater rearing habitats in non-natal streams. It is unclear from this work whether the non-natal streams represent smaller streams that are unsuitable for spawning or larger river deltas.

Other Salmonids

While we did not find any direct evidence to suggest HSME occurs in other salmonid species beyond those discussed above, specifically sockeye salmon (*O. nerka*), we acknowledge that this does not necessarily preclude the behavior in these species. However, we may infer that the likelihood, or lack thereof, of HSME given what is known about these species and their life history and migratory strategies. Sockeye salmon are somewhat unique in that they typically rely on lacustrine habitats during early life history. Although variation exists across the range of sockeye salmon with respect to the degree to which certain populations or individuals rely on lakes, most juveniles migrate to sea after an initial year in freshwater and likely migrate quickly to the ocean. It should be noted that behaviors like what we define as HSME have been observed in sockeye salmon but do not meet our criteria based on our definition of natal watershed (Tabor et al. 2011, Griffiths et al. 2013). Lastly, we have not included the occurrence of cutthroat trout (*O. c. clarkii*) or bull trout (*Salvelinus confluentus*) within non-natal habitats which may be the result of two potential reasons. First, observations are typically of adult and sub-adult life stages. And second, entry into brackish and potentially non-natal habitats was limited in duration and not necessarily indicative of longer-duration rearing (Goetz et al. 2013, 2021). We acknowledge the potential for HSME as we have defined to be expanded to include additional species where applicable.

HSME within habitat classes

Large River Deltas

Large river deltas are commonly associated with natal rearing for juvenile Chinook and chum salmon, although recent research has indicated an elevated level of non-natal use within these habitats among adjacent populations (Tuohy et al. 2018, Chamberlin 2022). Within the Stillaguamish delta, only 20% of fish analyzed originated from the Stillaguamish River whereas 60% of juvenile fish were of Skagit River origin and 16% from the Snohomish River (LeMoine et al. 2022). Similar results were reported across four years of monitoring within the Snohomish River delta (Chamberlin 2022). Within the lower delta, nearly half of the fish encountered during estuary monitoring in some months were of Skagit River origin. The timing and size of the fish encountered suggest that the Skagit origin fish likely moved, whether volitionally or not, as fry from their natal delta to suitable habitats within the Snohomish. Recent work in the Nisqually River delta in south Puget Sound also found that juvenile Chinook salmon in the delta originated from three basins and nine rivers in Puget Sound, including from 14 hatcheries (Hayes et al. 2019). In the Nisqually delta, roughly a quarter of juvenile fish did not originate from the Nisqually River. Most of the non-natal fish were from the nearby Puyallup River but as far as the Green and Skykomish Rivers of Central and Northern Puget Sound, respectively.

Embayments

Observations of juvenile salmonids in embayment were widespread across the Whidbey Basin of Puget Sound (Beamer et al. 2003, 2006, Kagley et al. 2007). Beamer et al. (2003, 2006) showed regular use of barrier estuaries by Chinook salmon fry migrants; because these pocket estuaries do not contain Chinook salmon spawning, fry must exhibit HSME to rear in these miniature watersheds. Across northern Puget Sound, Chinook salmon fry were observed in roughly 80% (19 of 24) of barrier estuaries that were sampled. Importantly, during peak outmigration periods, Chinook salmon density was 52% higher in pocket estuaries than adjacent nearshore habitats. This suggests a preference for barrier estuaries as higher quality rearing habitats. Additional observations indicated that Chinook salmon densities in barrier estuaries could be 10 and 100 times greater than other nearshore and offshore habitats, respectively (Beamer et al. 2003). These densities may reflect the importance of these habitats due to a lower abundance of predators, thermal conditions that benefit growth, and a higher food availability. In Hood Canal, seine surveys from February to July found nearly 7,000 summer chum juveniles extensively using habitats – particularly saltmarsh lagoons – throughout Dabob Bay, an embayment with no documented summer chum spawning (Bahls 2004). The Dabob Bay observations are noteworthy because they suggest summer chum juveniles may leave natal spawning ground within days or several weeks of emergence and spend multiple months rearing in non-natal estuarine habitat. Additional extensive surveys in Hood Canal found that the relative abundance of chum fry was highest in pocket beaches and barrier lagoons compared to adjacent nearshore and natal habitats (Tuohy et al. 2018). This was especially true for juveniles from summer-run chum populations in the region. Interestingly, although most fish observed in barrier estuaries were of sizes indicative of fry, Kagley et al. (2007) reported that individuals of several species observed in such habitats were larger than those occupying adjacent nearshore habitats in some locations.

Small Coastal Streams

Roughly a decade ago, some of the first data on HSME in small, non-natal coastal streams in salmon emerged from the Whidbey Basin. Beamer et al. (2013) electrofished 63 small coastal streams that drain into the Whidbey basin. Over half (n = 32) contained juvenile Chinook salmon, largely from January to May. Interestingly, from January through April the body size of these juvenile Chinook was similar to or larger than other juvenile in nearby nearshore habitats. Juvenile Chinook occurrence in small coastal streams began in January, peaked in February or March, and declined in April and May, reflecting a 33-42 day residence time which is similar to observations in barrier estuaries and scrub shrub delta habitats in natal Skagit River delta. Growth of juvenile Chinook in these small coastal streams was similar to what is observed in pocket estuaries but less than the various wetland zones present in natal Skagit River delta habitat. This study found that smaller streams with ~ 45-hectare watersheds were associated with juvenile Chinook presence and that streams further from Chinook-bearing streams and small streams with steeper slopes had a reduced presence of juvenile Chinook. Importantly, the presence of a culvert in the stream was associated with reduced Chinook occupancy; although this correlation cannot determine whether culverts impede or block juvenile movement upstream, the pattern is important to explore further for potentially improving fish use of these rearing habitats.

Additionally, recent work in the Whidbey Basin found that restoration can provide juvenile Chinook new access to non-natal coastal streams for rearing. Henrichs and LeMoine (2022) report on restoration work on Crescent Harbor Creek in north Whidbey Island. This restoration effort relocated the creek channel, thereby increasing the stream length and decreasing its gradient as the stream enters a 206-acre tidal channel wetland. The historical stream channel had a shortened channel length, high flow velocity, and high incision due to diking and diversion. Electrofishing in the relocated channel yielded salmonids, sculpins, and various estuarine fishes. Of the salmonids, juvenile natural origin Chinook were the most

abundant. The 52 juvenile Chinook captured in the restored creek were largely found in the most downstream areas of the restoration area, although juvenile Chinook were also observed in the upstream portions of the creek, including in the late rearing season. Interestingly, in the monitoring year (2022), juvenile Chinook salmon outmigration abundances were at record lows and so in larger outmigration years small coastal streams like this would likely be more populated by these fish due to density-dependent competition for natal rearing habitat. Juvenile chum and coho were also found throughout most of the restored creek, although it is unclear if these species are natal in origin. Most importantly, the change in gradient after restoration allowed juvenile Chinook to use the entire stream reach which did not occur previously.

Beyond the Whidbey Basin, recent pre-restoration monitoring found Chinook fry and parr using the lower reaches of McSorley Creek, a small coastal stream in Des Moines, King County (Kubo 2022). Although coho and chum spawn and rear in McSorley Creek, Chinook do not spawn in this stream and so must have entered the stream after leaving their natal watershed and migrating through the marine environment. Planned restoration actions in the lower reaches of McSorley Creek may enhance available rearing opportunities for Chinook (Kubo 2022).

Bennett et al. (2014) studied coho emigrating from multiple streams on the northern Olympic Peninsula and the contribution that fall/winter age-0 fry migrants to the returning adult population. Roughly one-third of the returning adults were comprised of these fry migrants. Although this study did not assess which rearing habitats these juvenile coho used, there have been observations from these streams that show that fry migrants enter the marine environment early and either re-enter their natal stream to rear or enter a nearby non-natal stream. In particular, Roni et al. (2012) found that juvenile migrants use westward (towards the Pacific Ocean) non-natal streams within hours or days of migrating. Thus, this work suggests that non-natal stream rearing may produce coho that contribute to the adult return.

Although surveys throughout Hood Canal found that summer chum occurred in higher abundances in barrier estuary habitat, fall chum showed an overall preference for small stream delta alluvial fans and delta channels (Tuohy et al. 2018). Therefore, beyond potential species differences in HSME, work in Hood Canal suggests intraspecific variation in the expression of HSME within a region. This underscores the importance of maintaining a portfolio or mosaic of rearing habitat variation to support a diversity of species and runs.

Finally, recent work used environmental DNA (eDNA) to survey for various fishes including multiple salmonids throughout western Washington, particularly the Puget Sound region (Glasgow and Jorgensen 2022; interactive web map¹). These eDNA results identified the presence of Chinook and coho salmon in small coastal streams in south Puget Sound and the Kitsap Peninsula where spawning is not known to occur. Of course, eDNA cannot quantify the abundance of these species nor the life stage, but these results could suggest a relatively widespread pattern of HSME in Puget Sound for Chinook and coho.

Discussion

Juvenile salmonids of diverse species, life histories/origins (run type, hatchery vs wild), and geographies exhibit HSME where fish disperse outside their natal watersheds, enter the marine environment, and re-enter freshwater or brackish rearing habitats in non-natal watersheds. Such behavior differs from the standard, relatively linear out-and-back model of salmon outmigration that is often considered where

¹ <https://wildfish.maps.arcgis.com/apps/webappviewer/index.html?id=2e397fb6c22c44b99b98c0e069acdf01>

juveniles rear in their natal watershed before transitioning to the ocean to mature and then returning to their natal watershed to spawn. Our review found HSME in at least seven species and three continents including Europe, Asia, and throughout western North America. Much of the evidence for HSME has been observed in small coastal streams but there is also important evidence of non-natal use within larger river deltas and brackish environments like barrier estuaries. This cumulative body of work suggest salmon may rely on an expanded mosaic of rearing habitats and that current recovery plans could benefit from including these alternative life history or migratory strategies within management actions. Below we explore potential drivers for HSME, the implications for salmon recovery, the role of non-natal habitats in restoration planning, and current regulations and practices surrounding non-natal habitat.

Why does HSME occur?

Non-natal habitat use is likely an adaptive behavior by which individuals deviate from the traditional sequence of habitats during early life stages. While evidence suggests some life history types are observed more often (e.g., fry migrants, sub-yearlings) to exhibit HSME, observations from Humboldt Bay and the Baltic Sea indicate the behavior is not exclusive to a particular life history strategy. To our knowledge there is no research that specifically addresses why HSME occurs, although we can speculate as to the potential drivers of this behavior. The question may be broken into two parts: 1) why would fish leave their natal habitats/watersheds, and 2) why would fish re-enter freshwater or brackish environments (HSME) in non-natal watersheds? The impetus behind initiating HSME may itself be an adaptive volitional response to density dependent habitat limitations or an alternative life history strategy for a given species/population (Apgar et al. 2020). An alternative and non-mutually exclusive explanation is that departing a natal watershed is a stochastic or neutral response to environmental conditions such as physical displacement by freshets and high river flows (Murray and Rosenau 1989). In either case, there is value in considering the opportunity provided by these alternative habitats and their ability to support individuals leaving their natal watersheds.

Density dependent processes can influence life history expression and dictate migratory strategies in salmonids (Greene and Beechie 2004). Such processes are generally predicated on habitat limitations that reflect reduced capacity due to the condition or extent of natal environments. Where these conditions exist, the prevalence of HSME behavior likely increases. The abundance of Chinook salmon fry migrants in the Skagit and Snohomish rivers is positively (linear) related to overall outmigration abundance, indicating that a density dependent response in freshwater may control the number of early migrants entering the downstream estuary and adjacent nearshore habitats (Beamer et al. 2003, Chamberlin 2022). Similarly, Apgar et al. (2020) found that smaller streams and high conspecific densities encourage higher rates of downstream non-natal habitat use. If the abundance of juvenile salmon exceeds the capacity of natal delta habitat, it may be expected that the prevalence of HSME will increase.

Beamer et al. (2006) observed a positive correlation between juvenile Chinook salmon densities in pocket estuaries within the Whidbey Basin and overall outmigration abundance in the Skagit River. At least within the Whidbey Basin of Puget Sound, the correlation between population abundance, high proportions of early migrants, and increased densities in non-natal habitats suggests that density dependent migration may influence the likelihood of non-natal habitat use when local natal habitat conditions are limited. However, these limiting natal habitat conditions do not remain static because annual and among-site variation in juvenile Chinook salmon density suggests that differences in outmigration abundances among natal rivers and between years influence the distribution of juvenile Chinook salmon (Beamer et al. 2006). Greene et al. (2021) found evidence of density dependence in several deltas within Puget Sound, although the magnitude and consistency varied considerably with

population size and habitat extent (Greene et al. 2021). As such the role of non-natal habitat is not exclusive to large populations but may also support cohorts where density dependent pressures are expressed at much lower population sizes because of limited natal habitat opportunities. Additionally, smaller population sizes may exhibit HSME because a simplified natal watershed may not have the adequate extent or spatial arrangement of refuge habitats available during natural disturbances. Therefore, it is likely important to consider population abundance, natal habitat conditions and extent, and life history diversity when assessing the likelihood for HSME and the importance of non-natal habitats across regions.

While conditions that create density dependence (e.g., abundance, habitat capacity/condition, life history expression) may influence the distribution and abundance of individuals exhibiting HSME, it is also valuable to consider the reasons why fish enter non-natal habitats rather than exhibit extended, albeit early, marine residence. The discrepancy between observed densities within non-natal habitats and adjacent nearshore shoreline habitats suggests a degree of preference for the former (Beamer et al. 2003, 2006, Kagley et al. 2007, Beamer et al. 2013). Habitat diversity is known to increase growth opportunities for juvenile salmonids during early life stages (Davis et al. 2019, Greene et al. 2021). The importance of growth during early life stages for salmonids may indicate that juveniles select rearing habitats with optimal conditions to enhance their growth potential and minimize mortality risk. Prey availability can vary considerably between February and June in nearshore habitats throughout Puget Sound (Kemp and Keister 2015, Beauchamp et al. 2018) and oftentimes lags production in estuarine environments (Woo et al. 2019). Similarly, thermal conditions in the nearshore often contrast with patterns in deltas and small streams due to the influence of freshwater (Hall et al. 2018). The result is warmer relative temperatures in the nearshore earlier in the season and cooler temperatures later. When coupled with prey availability, non-natal habitat conditions may be preferable in early months and nearshore conditions later in the season (Connelly et al. 2018). Lastly, refuge from predation may also play a role in use of non-natal freshwater and brackish habitats. Predation on juvenile salmonids in nearshore habitats is widespread and can be considerable in some locations or time periods (Duffy and Beauchamp 2007, Duncan and Beaudreau 2019). Several studies reported lower densities or occupancy of predator species in barrier estuaries and small coastal streams (Beamer et al. 2003, Kagley et al. 2007, Beamer et al. 2013). Thus, although HSME may be stimulated by density-dependent habitat limitations or stochastic responses to environmental disturbances, the use of non-natal habitats beyond the natal watershed is likely an adaptive mechanism to improve juvenile growth and survival prior to entering the marine environment.

Potential Implications for Salmon Recovery

Our review suggests that HSME is widespread among regions and species. Additionally, HSME appears to be relatively common in some regions and species such as Puget Sound Chinook salmon. However, the fate of individuals that exhibit HSME and their contribution to population productivity remains unclear yet may have important implications for salmon recovery. In the past, early (fry) migrant Chinook salmon and/or coho salmon have been considered ‘surplus’ fish that contribute little to the returning adult population. However, recent research has shown that these early outmigrants, including individuals that exhibit HSME, may represent an important life history strategy that can contribute over 20% of the returning adults to a particular population (Bennett et al. 2014, Sturrock et al. 2015, Campbell et al. 2023). Although it remains unclear what proportion of early outmigrant fish that have undergone HSME return as adults, it should not be assumed that these fish are inconsequential with respect to population productivity.

HSME opens additional questions about the potential for this phenomenon to contribute to straying in the adult life stage. Imprinting to natal environments is typically believed to happen during smoltification (Quinn 1993). As such, it is unclear if smoltification in fish exhibiting HSME results in non-natal fish returning to their natal watershed or to non-natal watersheds used during early life stages (see Hansen and Jonsson 1994). Koski et al. (2009) observed non-natal use of a small coastal stream by coho salmon where these juveniles imprinted on the non-natal stream and returned to successfully spawn. Taal et al. (2017,2018) also questioned whether HSME could potentially allow for salmon to colonize new streams or recolonize extirpated streams and permit genetic mixing among populations, thereby supporting resilience. However, it is also possible that HSME allows salmon to imprint upon non-natal habitats that are unsuitable for spawning; although these fish may not contribute to subsequent generations, they may still be ecologically beneficial as prey for other species (people, orcas, birds, etc.) or by providing marine derived nutrients to the landscape (Naiman et al. 2002). The different potential consequences of HSME for staying likely depend on the spawning conditions required by different populations or species. Overall, it is worth considering the potential implications of this behavior and these habitats while also recognizing that the significant impacts to estuaries and small coastal streams across the Pacific Northwest have likely substantially constrained opportunity for this behavioral expression.

Restoration and Protection of non-natal habitats

Given the evidence for HSME and the potential implications for population recovery, it may be valuable to consider how non-natal rearing habitat fits into regional restoration and salmon recovery planning. To our knowledge, there is no systematic framework for evaluating the role and benefits of HSME-relevant habitats and their relevance to particular populations. Even so, some entities show a growing interest in protecting and restoring HSME-relevant habitats (e.g., Beamer et al. 2005). Although some regional prioritization of these habitats exists, it is often unclear how particular small coastal streams or embayments are strategically assessed. Because restoration resources are limited, prioritization strategies that account for potential benefits to a given population or species may be particularly effective.

The lack of a systematic focus on HSME and non-natal rearing habitats may be a consequence of ‘shifting baseline syndrome’ where subsequent generations continuously recalibrate their understanding of ecological baselines to their own lived experiences. In fisheries, this was recently illustrated with multiple forage fish species in Canada. Specifically, forage fish stocks were shown to have collapsed within decades of the first European settlers impacting habitats and not later in the mid-20th century when these fisheries were recognized as in decline (Morin et al. 2023). In environments like Puget Sound, small coastal streams and pocket estuaries may have been among the first habitats to be profoundly impacted by Euro-American settlement due to their smaller sizes. Indeed, these small streams and estuaries were widely influenced by the first settlers for private and early commercial practices (Morgan 1979). As such, a pronounced decrease in HSME by salmon may have occurred in the late 1800’s, far before widespread salmonid research and protections in the region. With such a decrease in HSME, population spatial structure and diversity would have been affected, reducing the resilience of the populations towards stressors that came to bear in the following centuries.

Compounding this shifted baseline is the broadly understood conceptual model for salmon life cycles. Under this model salmon spawn, rear in natal watersheds, mature in marine environments, and return to natal watersheds to spawn. Under this model, many researchers and conservation practitioners would have little reason to assess non-natal rearing habitats outside of natal watersheds, thus limiting the potential for detecting HSME if it were occurring. In conjunction with diminished habitat quality or a lack of habitat accessibility, the assumption that juvenile fish do not exhibit HSME would be reinforced by a

dearth of fish using non-natal habitats to rear. This may be particularly true because non-natal rearing is likely (at least in part) a density dependent phenomenon and so would be harder to detect with small population sizes and/ or in low outmigrant years. The potential early loss of non-natal watershed habitats in the 1800's and early 1900's could have contributed to depressed salmon populations and, along with density dependent use of non-natal habitats, potentially led to a positive feedback loop where juvenile fish could not access these habitats, making it more challenging to detect the phenomenon of HSME, and resulting in a dearth of relevant protections and research. Although speculative, it may be that intentional research targeting HSME, particularly after restoring fish passage and habitat quality, may find that HSME is more prevalent than we found here, particularly in years when outmigration numbers, and therefore juvenile densities, are higher. Indeed, HSME may become more common if and when salmon stocks recover.

HSME underscores the importance of maintaining and enhancing abundant and diverse non-natal habitat – rather than just habitat in the natal watershed – as part of the portfolio of rearing habitats. Including non-natal habitats in current versions and future revisions of recovery plans would likely be fruitful but would likely benefit from being guided by a regional framework that considers the spatial arrangement of habitats and both current and desired future conditions for habitat and populations (McBride and Beamer 2010a, b). Understanding habitat conditions and prioritizing restoration in natal watersheds is common in regional recovery plans, but extending these assessments *outside* watershed boundaries is relatively nascent. Combining regional habitat status and trends information for non-natal habitat classes/features with recovery goals and restoration plans could prove useful. Beamer et al. (2003) underscored how the 12 pocket estuaries in Skagit Bay were degraded or inaccessible to non-natal juvenile salmon rearing while highlighting that nearly 90% of the pocket estuary habitat was inaccessible to salmon fry and normal tidal hydrological processes due to tide gates, roads, and other anthropogenic impediments. Similarly, for small coastal streams, many of which support juvenile salmonids, infrastructure can severely limit access, potentially trap juvenile fish, and adversely impact habitat conditions upstream of the barrier (Beamer et al. 2013, Greene et al. 2017). Yet, our review found that when these barriers are removed and habitat was restored, non-natal use by juvenile salmonids has been observed and expanded compared to pre-restoration conditions. Further assessments and development of a framework evaluating the benefit to Chinook salmon for restoring fish passage at small coastal streams and embayments is critical (Schlenger et al. 2018, Bloch et al. 2019, ESA et al. 2022).

When assessing the habitat classes that juvenile salmon use when expressing HSME, recovery planning could also consider the spatial arrangement of non-natal habitats and how spatial arrangement may affect the overall opportunity to support HSME (**Figure 2C**). Within Puget Sound, the distribution of distinct habitat *features* within our defined habitat classes is variable (Collins and Shiekh 2005, Shipman 2008) suggesting an inclusive approach to protecting non-natal habitat and sub-regional prioritization. For example, while small coastal streams and barrier beaches may be prevalent in Whidbey Basin, small estuaries formed within glacial depressions may be more common in south and central Puget Sound. These features support HSME but their importance for protection or restoration may vary regionally. It may also be important to consider the spacing or frequency of non-natal opportunities relative to natal population sources when planning restoration or protection. While a distance threshold for non-natal habitat use remains uncertain, it is likely that opportunity for HSME is reduced for habitats that are farther from the natal source (**Figure 2B**). As individual fish travel farther and/or for longer periods of time, we expect the need for non-natal habitat diminishes as fish grow larger and become further acclimated to marine environments following the natural transition from nearshore to offshore during the early marine period (Duffy et al. 2005, 2010). Spatial arrangements of available non-natal habitats can likely have

some influence on the HSME-distance relationship. Lastly, accounting for shoreline condition between natal sources and non-natal habitat is potentially important when assessing potential HSME by juvenile salmonids. Degraded shorelines (e.g., armored, overwater structures) can have noticeable impacts on fish migration, predator abundance, and habitat function that results in fish avoiding and/or experiencing increased mortality and reduced growth (Munsch et al. 2016, 2017). Evaluating non-natal habitat for inclusion in recovery or restoration planning would benefit from considering these features in the context of the migration corridor rather than in isolation. This may be particularly important if restoration actions in migratory corridors improves fish access to non-natal habitats that have high potential for rearing.

Example of Non-natal Habitats in Current Regulations and Practices

The habitats used by salmon exhibiting HSME are, in part at least, already accounted for in existing regulations, including legal authorities from federal to state and local levels. For instance, at the federal level, Section 401 of the United States Clean Water Act requires permits for fill material in waters of the United States which includes the stream and marine habitats used by salmon undergoing HSME. Further, in its habitat valuation for characterizing impacts and avoidances measures for projects that adversely affect ESA-listed Chinook and chum salmon habitat, NOAA credits higher values to habitats within 5 miles (~ 8 km) of natal river mouths for listed salmonids in addition to estuaries and other embayments (Ehinger et al. 2015, 2023). This certainly accounts for some non-natal habitats encountered by HSME but may not account for non-natal habitats potentially available to juvenile salmon that may be further from their natal river or for rivers with non-listed salmon species that also use non-natal habitats. Even so, this ~8 km criterion likely serves to bolster juvenile salmon dispersal “corridors” used by fish to move between natal watersheds and putatively higher-quality rearing habitats in embayments and small coastal streams than would otherwise be found along other nearshore environments.

At the state level, policies like Washington’s Shoreline Management Act and the Growth Management Act can also account for HSME-relevant habitats. WDFW’s Priority Habitats and Species list that is used by various local jurisdictions and other conservation entities already includes coastal embayments and instream habitats which encompass the habitats used by salmon exhibiting HSME. As such, future guidance could incorporate non-natal rearing habitat use as cities and counties continue to address their planning requirements. Beyond these legal frameworks, under Chapters 77.55 RCW and 220-660 WAC, any person wanting to conduct a hydraulic project must first obtain a Hydraulic Project Approval from WDFW to ensure that the project is done in a manner that protects fish life. A hydraulic project is the construction or performance of work that will use, divert, obstruct, or change the natural flow or bed of any of the salt or fresh waters of the state. Specifically, WAC 220-660 highlights the “migration, rearing, and feeding areas for juvenile salmon” as a saltwater habitat of special concern when considering proposed project impacts and permit conditions. Further, the requirement for fish passage and access is referenced throughout WAC 220-660 regarding in-water work, dredging, water crossing structures, fish passage improvement structures, etc. In particular, water crossing structures of waters of the state are subject to WAC 220-660, with a few exceptions noted therein, which stipulate that the design and construction of structures provide “unimpeded fish passage” or “the free movement of all fish species at *any mobile life stage* around or through a human-made or natural structure”.

Additionally, RCW 77.95.180, the section governing the Fish Passage Barrier Removal Program, requires WDFW and Washington Department of Transportation to identify and ameliorate fish passage barriers caused by state roads and highways “based on the principle of maximizing habitat recovery”. WDFW therefore assesses fish passage barriers and provides technical guidance to restore stream habitats. WDFW’s ‘Fish Passage Inventory, Assessment, and Prioritization Manual’ defines “fish use potential” as “the potential for *adult* salmonid use at an instream feature; a determination of ‘potential fish habitat’ is

not intended to be an indicator of usability for all fish species and life stages” (Washington Department of Fish and Wildlife 2019). Even though this definition may be limiting to the upstream migration of juvenile salmon displaying HSME, the manual’s barrier priority index and screening priority index do account for highly mobile anadromous species, federal listing status, and whether a project could potentially improve landscape connectivity for rearing or out-migrating juveniles. As such, fish passage and screening considerations can account for juvenile salmon movement into and out of smaller, non-natal streams and estuaries. Even though WDFW’s manual largely emphasizes non-tidal sections of streams, emerging recommendations are forming to account for tidal fish passage barriers, including for juvenile salmon (Greene et al. 2017, ESA et al. 2022, Smith et al. 2023). Finally, the barrier and screening priority indexes incorporate rearing habitat gain for juvenile fish and do not differentiate fresh or salt water. Therefore, habitats used under HSME would be considered as part of rearing habitat gain (Daniel Barrett and Christy Rains, *personal communication*).

Beyond the brief guidance provided in Appendix D of WDFW’s Water Crossing Design Guidelines (Barnard et al. 2013), there is currently limited guidance for tidal environments to enhance fish access. Various impediments for fish access to HSME-relevant habitats include an expansive network of shoreline roads that are built waterward as well as tidal barriers like dykes. Existing and extensive railroad crossings have been identified as a potentially substantial barrier to numerous non-natal salmon habitats (Bloch et al. 2019, ESA 2022). Under the Interstate Commerce Commission Termination Act of 1995, only the Surface Transportation Board has jurisdiction over railroads regarding land use and environmental issues (see *City of Auburn v. U.S. Government*, 154 F.3d 1025, 1998). Regardless, ongoing collaborative conversations between BNSF Railway, the Tulalip Tribes, WDFW, and other jurisdictions and conservation groups are working to identify and restore non-natal habitats for juvenile salmon using innovative recommendations for tidal barriers. A recent assessment of the BNSF railroad by this collaboration suggested that larger replacement structures that discharge at grade and which are either box culverts or short trestles would be improvements to juvenile fish access of non-natal habitats (Bloch et al. 2019). Further, the BNSF railroad assessment emphasized that sea level rise and climate change will likely exacerbate the impact of the railroad on juvenile salmon access to these non-natal habitats. This work culminated in developing programmatic recommendations for restoring coastal estuaries and streams along the railroad and provided conceptual designs for three of 45 of the identified priority stream crossings (ESA 2022).

To our knowledge, restoration work to improve juvenile salmon fish passage into non-natal small coastal streams and embayments is relatively limited, although there is growing interest. Emerging work, such as the BNSF railroad assessment and work on tidal fish passage restoration (ESA 2022, Smith et al. 2023), provides a useful framework to initiate restorative actions for a potentially expansive amount of rearing habitat not only in association with railroad but also with shoreline roads, dykes, and other infrastructure. The various and sometimes overlapping jurisdictions that have authority over these roads and other tidal barriers may benefit from considering the potential restoration and protection of non-natal rearing habitats. Existing laws for regulated federal and state waters apply to non-natal habitats, yet HSME-related habitats for salmon are likely more challenging to assess, prioritize, regulate, and restore than larger natal habitats (Washington Department of Fish and Wildlife 2019, ESA 2022). Explicit consideration of the potential value of small coastal streams, embayments, and large river deltas as non-natal rearing habitats could aid implementing existing regulations and restoration prioritization for fish use.

Remaining uncertainties and data gaps

We anticipate that observations of HSME may be more common than have been reported in scientific journals and the gray literature. Additionally, we expect that intentional observations for HSME may uncover this phenomenon in more species and locales. As such, we encourage salmon practitioners and researchers to report observations of HSME and to develop targeted studies on HSME. Although we found considerable evidence for HSME across species and geographies, there remain uncertainties that require further research attention. We provide a list of proposed questions or research topics that could improve our understanding of HSME, inform policy decisions, and reduce uncertainty around potential mechanisms that influence the presence and magnitude of the behavior.

- How much do fish exhibiting HSME contribute to population productivity?
- Does HSME contribute to genetic mixing among populations/watersheds?
- Does HSME contribute to straying and/or stream (re)colonization?
- Can we predict the likelihood or magnitude of HSME with information on population abundance, natal habitat condition, and non-natal habitat opportunity?
- What is the relationship between distance from source population and the presence of HSME? Is there a threshold distance where HSME becomes unlikely?
- Does the spatial arrangement of non-natal habitats (saturation vs. absence) influence the relationship between HSME and distance from natal source?
- Does shoreline condition between a natal watershed and potential non-natal habitat influence presence or magnitude of HSME?
- Can we quantify whether HSME occurs volitionally (i.e., density dependent) versus stochastically (e.g., due to freshets)?
- Can current fish monitoring programs capture HSME? Does HSME confound interpretations of current fish monitoring programs?
- Do species with extended rearing times (e.g., coho) display HSME more frequently than species which migrate to the ocean more quickly (e.g., chum)?
- What is the duration of residence in non-natal habitats used during HSME? Are juvenile salmon rearing in these habitats for longer durations or ephemerally passing through these habitats.
- All populations likely benefit from non-natal habitat protection and restoration, but how do we account for shared benefits from a given non-natal habitat to multiple populations and jurisdictions, particularly when local jurisdictions tend to lead management of natal watersheds?

Conclusions

Our review underscores the prevalence of juvenile salmon rearing in non-natal habitats beyond their natal watersheds across geographies and species. This non-natal rearing via habitat shifting through the marine environment has important implications for salmon recovery. In particular, this phenomenon is expected to be most pronounced when outmigration densities are large, natal rearing habitat is limiting, and life history diversity of juveniles is skewed toward fry migrants (Beamer et al. 2006, Wallace et al. 2015, Apgar et al. 2020). Where these conditions occur, regulations and actions directed toward these non-natal strategies and habitats could prove critical for supporting abundance and productivity as well as maintaining population diversity. As such, continued recovery of salmon stocks could be constrained if these efforts do not encompass restoration of rearing habitats in non-natal watersheds. Accordingly, proactive restoration of non-natal rearing habitats may be an important step to fully realize salmon recovery. Non-natal coastal streams and embayments likely add to the portfolio or mosaic of rearing habitats available to juvenile salmonids as they migrate from spawning grounds to the marine

environment. Continued investment into research and recovery of environments suitable for HSME is important to help understand and quantify the relative value of these systems to salmon life histories and recovery.

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