

Technical Report 2012-6

**A REVIEW OF ADULT SALMON AND STEELHEAD STRAYING
WITH AN EMPHASIS ON COLUMBIA RIVER POPULATIONS**

**Prepared by:
Matthew L. Keefer & Christopher C. Caudill**

**Department of Fish and Wildlife Resources
College of Natural Resources, University of Idaho**



**Prepared for:
U.S. Army Corps of Engineers
Walla Walla District**

FINAL

Technical Report 2012-6

**A REVIEW OF ADULT SALMON AND STEELHEAD STRAYING WITH
AN EMPHASIS ON THE COLUMBIA RIVER BASIN**

**Prepared by:
Matthew L. Keefer & Christopher C. Caudill**

**¹Department of Fish and Wildlife Resources
College of Natural Resources, University of Idaho**

**Prepared for:
U.S. Army Corps of Engineers
Walla Walla District**

**Under contract #:
W912EF-08-D-0007**

FINAL

TABLE OF CONTENTS

EXECUTIVE SUMMARY	v
ACKNOWLEDGEMENTS	viii
1.0 INTRODUCTION AND METHODS	1
2.0 HOMING AND STRAYING IN CONTEXT	2
2.1 EVOLUTIONARY CONTEXT.....	2
2.2 ECOLOGICAL CONTEXT	3
2.2.1 HABITAT EFFECTS	4
2.3 MANAGEMENT CONTEXT	5
2.3.1 DONOR VERSUS RECIPIENT POPULATIONS.....	5
3.0 HOMING MECHANISMS	8
3.1 ROLE OF GENETICS	8
3.2 ROLE OF PHYSIOLOGY AND BEHAVIOR	8
3.3 JUVENILE IMPRINTING	9
3.3.1 WHAT ODORS ARE USED FOR IMPRINTING?	10
3.3.2 WHEN DOES IMPRINTING OCCUR?	10
3.3.3 MULTIPLE / SEQUENTIAL IMPRINTING	10
3.3.4 HOW DOES IMPRINTING OCCUR?	12
3.3.5 IMPRINTING EXPERIMENTS	13
3.4 ROLE OF PARR-SMOLT TRANSFORMATION AND OUTMIGRATION	15
3.5 ROLE OF HATCHERY REARING.....	15
3.6 ADULT HOMING	16
3.6.1 ADULT HOMING MIGRATION PHYSIOLOGY	17
3.6.2 ADULT HOMING BEHAVIOR: MIGRATION CORRIDORS	18
3.6.3 ADULT HOMING BEHAVIOR: EXPLORATION AND TESTING.....	20
4.0 ADULT STRAYING	22
4.1 DEVELOPING A STRAYING LEXICON	22
4.1.1 THE CHALLENGE OF SPATIAL SCALE	22
4.1.2 THE CHALLENGE OF IDENTIFYING STRAYS	23
4.1.3 DONOR VERSUS RECIPIENT POPULATIONS.....	23

4.1.4	PERMANENT VERSUS ‘TEMPORARY’ STRAYING	24
4.2	STRAYING MECHANISMS	26
4.2.1	INCOMPLETE JUVENILE IMPRINTING.....	26
4.2.2	INTERRUPTED JUVENILE IMPRINTING	27
4.2.3	ADULT SENSORY FAILURE.....	27
4.2.4	ADULT MEMORY FAILURE	28
4.2.5	REPRODUCTIVE BEHAVIOR / DENSITY DEPENDENCE	29
4.2.6	GENETIC & LIFE HISTORY EFFECTS.....	29
4.2.7	ATTRACTIVENESS OF NON-NATAL SITES.....	31
5.0	SYNTHESIS OF STRAYING DATA	32
5.1	DATA CHALLENGES	32
5.2	GENERAL PATTERNS	32
5.3	DONOR POPULATION STRAY RATES: COLUMBIA RIVER BASIN	35
5.3.1	FALL CHINOOK SALMON.....	35
5.3.2	SPRING CHINOOK SALMON	36
5.3.3	COHO SALMON.....	38
5.3.4	SOCKEYE SALMON	38
5.3.5	STEELHEAD	39
5.4	DONOR POPULATION STRAY RATES: NON-COLUMBIA SITES.....	39
5.5	RECIPIENT POPULATION STRAY RATES.....	40
5.6	HATCHERY AND OUTPLANTING EFFECTS.....	42
5.7	JUVENILE TRANSPORTATION EFFECTS ON STRAYING	43
5.7.1	TRANSPORTATION STUDIES.....	43
5.7.2	TRANSPORT-STRAYING MECHANISMS	45
6.0	MODELING ADULT STRAYING BY SNAKE RIVER STEELHEAD	48
6.1	MODEL DESCRIPTION.....	48
6.2	EXAMPLES OF MODEL OUTPUTS.....	49
6.2.1	BASIN-WIDE STRAY RATE ESTIMATES.....	49
6.2.2	SINGLE RECIPIENT POPULATION ESTIMATES	51
7.0	LITERATURE CITED	54

Cover photo credit: C. Caudill

EXECUTIVE SUMMARY

Context for review – Management of the Federal Columbia River Power System (FCRPS) includes collection of juvenile salmonids at dams followed by downstream transport on barges or trucks. Evidence from tagging studies indicate higher straying rates in adults that were transported as juveniles compared to those that migrated in river, potentially hindering salmon and steelhead recovery efforts. A clear understanding of the patterns of straying across populations and the underlying mechanisms affecting upstream migration behavior, route selection, and homing to (or straying from) natal habitats is critical to evaluating the effects of “natural” versus human-induced straying on salmon and steelhead populations. A comprehensive review and analysis of available literature and data is currently lacking for the Columbia River-Snake River system.

This literature review presented here is intended to provide managers with an overview of available information on the many inter-related mechanisms associated with juvenile imprinting and emigration and subsequent homing and straying behaviors by returning adults. The review includes a synthesis of published straying data from the Columbia River basin, with additional comparison data from representative studies outside of the Columbia system. Topics covered in the review and data synthesis were developed in consultation with U.S. Army Corps of Engineers (USACE) biologists as part of a coordinated effort to identify critical knowledge gaps and to provide a context for prioritizing research and management needs. In the review, we identified potentially important demographic and genetic factors affecting both donor populations (populations strayed from) and recipient populations (populations receiving strays).

Snake River steelhead straying model – This review also includes results from a Snake River modeling exercise that was developed in parallel with the literature review. The model estimates the number of adult steelhead strays for donor and recipient populations across a range of adult straying rates, smolt abundance at Lower Granite Dam, transportation rate from the Snake River, and smolt-to-adult returns (SARs) for hatchery, wild, in-river, and barged populations. Model outputs indicate that transported hatchery steelhead contribute the largest number of strays in most simulations. The absolute number of strays also tended to increase with smolt abundance, as SAR’s increased, and as transport proportion increased. As part of the modeling exercise, we developed a simple numerical model to show the proportion of strays in a wild recipient population (i.e., relative abundance) in relation to donor population size, recipient population size, and donor stray rate. This model shows that strays from large donor populations can numerically overwhelm native fish in small recipient populations, even at low (~1%) stray rates.

We developed the model into a spreadsheet-based tool provided as a product of this project. This tool allows users to input a variety of data on Snake River steelhead juveniles and adults that are then used to estimate adult Snake River steelhead straying. The tool allows users to estimate total steelhead stray abundance and to estimate the number of strays that enter individual recipient populations (e.g., into the John Day River) using combinations of empirical values from recent years (i.e., from the Fish Passage Center) or user-specified values. The straying model is ultimately designed to help evaluate the potential effectiveness of different management efforts to reduce straying by barged fish.

Key conclusions – The content of the review has direct management implications for those working with adult salmon and steelhead straying in the Columbia River basin. Key findings include:

- adult straying is a desirable and ‘natural’ component of salmonid metapopulation biology in unmanipulated systems, and is critical to genetic resilience, demographic stability, and range expansion into unexploited habitats;
- adult straying rates differ among salmonid species;
- adult straying rates differ among populations and among life history types within species;
- most strays enter sites that are geographically close to natal sites; transported fish, however, often stray into more distant rivers;
- the effects of straying differ between the donor and recipient populations. Strays can have positive, negative, or neutral effects on recipient populations, depending on the source and relative abundance of the strays; effects on donor populations depend on straying rate and donor population size;
- adult straying is often associated with juvenile behavior and physiology – and especially olfactory imprinting – but migratory and reproductive behaviors of adults also influence homing outcomes;
- transportation of juvenile salmon and steelhead can increase adult straying behaviors, likely by negatively affecting sequential olfactory imprinting;
- hatchery rearing can contribute to adult straying, although there have been few spatially- and temporally-controlled studies of straying by closely-related hatchery and wild populations;
- in the Columbia River basin, many adults stray from the Snake River and enter mid-Columbia River tributaries, especially the Deschutes and John Day rivers; straying rates are higher for adults that were transported as juveniles; additional straying occurs at a variety of spatial scales basin-wide;

Critical uncertainties – The review identified several uncertainties related to managing ‘undesirable’ (i.e., human influenced) adult straying in the Columbia River basin. These include:

- the specific mechanisms of impaired imprinting for transported juveniles remain unknown; candidate hypotheses include chronological effects (i.e., transport is too rapid), spatial effects (i.e., barges are in inappropriate habitats), and in-barge effects (i.e., stress, contaminants, etc.);
- potential interactive or cumulative effects of hatchery rearing and juvenile transport are poorly understood;

- evidence suggests that strays may outnumber natives in small recipient populations; it is unknown how the impact of straying differs across donor and recipient population sizes;
- accounting for hatchery- and transport-related strays in the Columbia River system is far from complete because strays are not routinely identified or monitored in most sub-basins;
- it is not known how many strays successfully breed in most recipient populations;
- adult strays appear to preferentially enter some recipient river systems, but not others; the mechanisms affecting this selective behavior are largely unknown;
- genetic, fitness, and other population-level impacts of strays (i.e., outbreeding depression, introgression, hybridization, domestication effects, reduced productivity, etc.) have not been addressed for most Columbia River populations.

ACKNOWLEDGEMENTS

We wish to thank Dean Holecek, USACE Walla Walla District for administering the prime contract between USACE and UC Davis (Agreement No. W912EF-08-D-0007) coordinating the Straying Workshop and associated SRWG meetings. This work was conducted through a subcontract administered by UC Davis (Agreement Number 201120677-01) and we thank Frank Loge and Halona Leung for assistance administering the contract. We also thank everyone who participated in the straying workshop and follow-up meetings; their input guided development of this document and the straying modeling tool. The Final report was improved by constructive comments on the Draft report from Doug Marsh, Glen Mendel, and Peter Westley.

1.0 INTRODUCTION AND METHODS

The primary objectives of this review are to: (1) review the scientific literature on homing and straying by adult salmon and steelhead (*Oncorhynchus* and *Salmo* spp.), including a sub-objective to provide regional managers a common lexicon for use in discussing straying-related issues; (2) provide a synthesis of available published data on straying by Columbia River populations; and (3) develop a spreadsheet-based tool for modeling straying by adult Snake River steelhead with an emphasis on the effects of juvenile barging.

The straying model can be used to estimate the total number of steelhead strays from the Snake River or estimate the total numbers of strays that enter single recipient populations (i.e., the number of strays that enter the Deschutes or John Day river). The latter model capability can calculate the proportion of Snake River strays relative to the native recipient population. The model can also be used to test the effects of potential management efforts to reduce straying by Snake River fish. For example, users could test how a 50% reduction in straying by barged steelhead would affect the absolute number of Snake River strays or the ratio of strays to natives in a recipient population like the Deschutes River. We present model results for a variety of steelhead outmigration scenarios in the last section of this report, and the model is available for interested readers at: <http://www.cnr.uidaho.edu/uiferl/Research.htm>

Literature for the review was initially collected by searching in a peer-reviewed database (Web of Science) and by searching for grey literature reports posted on USACE, Bonneville Power Administration (BPA), Oregon Department of Fish and Wildlife (ODFW), and Washington Department of Fish and Wildlife (WDFW) websites. We emphasized peer-reviewed documents over grey literature whenever possible and used the most recent report when agency studies included multiple annual reports.

We used the citation lists in the most relevant papers and reports to identify material not found in the initial searches, and attempted to locate additional electronic files using Google Scholar. Relevant unpublished reports and those unavailable in electronic form were also solicited from personnel at the various agencies conducting relevant juvenile and/or adult salmonid research and monitoring in the basin. Information from the reviewed papers and reports were organized into several basic categories (i.e., juvenile imprinting, adult migration behaviors, straying mechanisms, etc.) and these were used to frame the synthesis.

There is a long history of research on the complex set of physiological and environmental factors that affect salmonid imprinting, homing, and straying. To help provide a concise summary of this multi-disciplinary work, we additionally relied on several previous reviews. We especially acknowledge the work by Hasler and Scholz (1983), Quinn (1984; 1993; 2005), Dittman and Quinn (1996), Dittman et al. (1996), Nevitt and Dittman (1999), Hendry et al. (2004), Pess (2009), and Ueda (2011, 2012).

2.0 HOMING AND STRAYING IN CONTEXT

2.1 EVOLUTIONARY CONTEXT

Homing to natal sites is a fundamental life history trait of most anadromous salmon and steelhead (*Oncorhynchus* and *Salmo* species). Homing increases the likelihood that reproductive-age fish will find mates and locate habitats that are favorable for both adult spawning and juvenile survival (Hendry et al. 2004; Quinn 2005). Return to natal sites is therefore highly adaptive, providing fitness benefits and contributing to the evolution of thousands of locally-adapted salmonid populations (Taylor 1991; Hendry et al. 2000; McDowall 2001; Waples et al. 2004). The spatial scale for homing varies among species, among populations, and within populations, ranging from very precise (i.e., within meters of natal sites; Stewart et al. 2003; Quinn et al. 1999, 2006, 2012) to broader habitat units like river reaches or river drainages (Candy and Beacham 2000; Bentzen et al. 2001; Hamann and Kennedy 2012).

Straying is also a critical evolutionary feature of adult salmonid behavior (Box 1). Although often described as a “failure to home” when viewed at ecological time scales – especially in the context of hatcheries and other human interventions – straying in wild populations can be adaptive over the short (ecological) or longer term (evolutionary/geological) time scales. Thus, it is useful to distinguish between proximate factors that affect straying (e.g., sensory ecology and physiological factors that affect orientation or changes in motivation to move upstream) from the ultimate (evolutionary) factors that have led to the evolution and maintenance of straying and to variation in straying rates among populations. The proximate factors are frequently thought to impact homing and increase straying (e.g., effects of barging), but a clear understanding of the ultimate factors is necessary to interpret straying rates and set management goals (e.g., what are “natural” straying rates). We

Box 1: Glossary of population biology

- **Adaptive / Adaptation:** traits or behaviors that are shaped by evolutionary processes / natural selection; adaptations contribute to survival and fitness
- **Metapopulation:** a single-species group of spatially-separated populations; some individuals interact through dispersal or inter-breeding
- **Donor population:** the source, or natal, population that produces dispersing individuals, including colonizers and ‘strays’ in the salmonid literature
- **Recipient population:** the non-natal population that receives strays
- **Dispersal:** process by which animals move away from their natal population
- **Proximate factors:** stimuli or conditions responsible for animal behavior at ecological time scales (i.e., immediate or short-term responses)
- **Ultimate factors:** evolutionary or genetic factors affecting animal behavior
- **Allee effects:** occurs when low population density limits population growth rate; also referred to as inverse density dependence or depensation
- **Demographic effects:** stochastic variation in reproductive and mortality rates, sex ratios, etc. is higher in small populations; result is higher extinction risk
- **Fitness:** a measure of survival and reproductive success across generations
- **Density dependence:** a variety of population processes, including reproduction and survival, can be affected by the abundance of individuals; many density dependent effects are negative (i.e., they can reduce fitness)

Box 2: Recent examples of anadromous salmonid range expansion & invasion

• Environmental change

Coho and sockeye salmon	Alaskan glacial retreat	Milner & Bailey (1989); Burger et al. (1997)
Multiple species	Arctic climate change	Stephenson (2006)
Atlantic salmon	Water quality improvement	Perrier et al. (2010)

• Intentional introduction

Chinook salmon	New Zealand	McDowall (1990); Quinn et al. (2001)
Multiple species	Laurentian Great Lakes	Mills et al. (1994); Crawford (2001)

• Accidental introduction

Chinook salmon	Argentina / Chile	Becker et al. (2007); Correa and Gross (2008)
Atlantic salmon	British Columbia	Volpe et al. (2000)

• Habitat modification

Coho salmon	Washington dam removal	Anderson and Quinn (2007)
Multiple species	Alaskan fishway installation	Bryant et al. (1999)
Pink salmon	British Columbia barrier removal	Withler (1982); Pess et al. (2012)

also note that straying occurs at the scale of the individual and population.

Straying buffers against spatial and temporal variation in habitat quality, allows colonization of new habitats (Box 2), and recolonization after local extinction. Straying also reduces inbreeding depression and density dependent effects such as competition among related individuals (Quinn 1993; Hendry et al. 2004). It is not clear whether some individuals within populations are genetically predisposed to straying versus homing, though it is likely that expression of these two strategies is in dynamic equilibrium in wild populations (Quinn 1984). Accumulating evidence suggests that a combination of predominantly philopatric individuals plus some strays makes for robust populations that can exploit favorable natal-site habitats, expand into new sites, and also disperse in the face of temporary or catastrophic environmental fluctuations. In fact, salmonids are commonly considered in terms of metapopulations connected by some degree of movement (i.e., straying) among populations.

2.2 ECOLOGICAL CONTEXT

Adult salmonids select spawning sites using a complex combination of heritable homing behaviors plus proximate behavioral responses to environmental and social cues (Dittman and Quinn 1996). As adults approach potential spawning habitats, they must simultaneously orient to natal sites and locate sites with suitable substrate, water temperature, water velocity, hyporheic flows, and other geomorphic features prior to spawning (Geist and Dauble 1998; Torgersen et al. 1999). They also must avoid predation, locate mates, defend against competitors, and successfully deposit gametes at the appropriate time. In some cases, adults must hold in suitable habitat for weeks to months prior to the onset of spawning; holding can occur at the eventual spawning location or in more distant staging areas. The degree of success in each of these ecological arenas ultimately drives reproduction and the evolution of locally-adapted traits and populations.

2.2.1 HABITAT EFFECTS

The relative stability and quality of spawning and rearing habitats can be a good predictor of homing or straying rates within a population. High site fidelity tends to arise when high-quality habitats are stable through time because such sites consistently attract adults and produce successful offspring (Quinn and Tallman 1987, 1989; Hendry et al. 2004). Site fidelity is typically lower where unpredictable inter- or intra-annual fluctuations in habitat quality or quantity result in lower mean survival or cohort failures (Quinn 2005; Cram et al. 2012).

Straying is one component of salmonid life history that varies within and among populations in response to habitat stability. Much like variation in juvenile residency times (Healey 1991), age at maturity (Groot and Margolis 1991; Fleming 1996), or the number of spawning events (i.e., iteroparity, Fleming and Reynolds 2004), straying can effectively “hedge” against habitat instability. Juvenile life history variation can result from genetic differences among individuals or expression of alternative behaviors or morphologies in response to environmental conditions (phenotypic plasticity) and has evolved to maximize survival to adulthood given the availability and predictability of suitable habitats. In comparison, variability in adult life history (e.g., age or number of spawning attempts) temporally spreads the risk of reproductive failure across years, and straying can spread the risk both temporally and spatially (LePage and Cury 1997; Quinn 2005). Importantly, the potential genetic and demographic benefits of straying cannot be realized if adults fail to reproduce. Failures occur when the non-natal habitat is unsuitable, when straying individuals fail to find mates, and when there are spatial or temporal mismatches between strays and local spawners that prevent breeding.

The proximate factors that make novel (i.e., non-natal) habitats attractive to strays have not been conclusively identified in the primary literature. However, it is likely that physical and chemical environmental factors and the spatial relationship between home sites and stray sites are the primary drivers. Environmental cues potentially include a variety of physiochemical properties of the non-natal site (e.g., discharge, temperature, chemical composition; Correa and Gross 2008; Ueda 2011) as well as behavioral or chemical cues from conspecifics (e.g., spawning activity, pheromones; Solomon 1973; Nordeng 2008).

Straying is not spatially random. Many case studies have shown that strays are exponentially more likely to enter rivers or tributaries near their natal site than to enter more distant drainages (Quinn and Fresh 1984; Labelle 1992; Unwin and Quinn 1993; Hard and Heard 1999; Thedinga et al. 2000; Schroeder et al. 2001; Jonsson et al. 2003; Correa and Gross 2008), though nearby sites are also more frequently surveyed. This presumably reflects a hierarchical homing process which identifies the coastal shelf, natal river estuary, natal river, etc. and the tendency for adjacent watersheds to have similar underlying geology, river morphology, and water quality parameters. Water chemistry may be of particular importance given that adult salmonids use olfaction for route finding and home site recognition (see Section 3.0).

2.3 MANAGEMENT CONTEXT

2.3.1 DONOR VERSUS RECIPIENT POPULATIONS

Demographically, straying fish affect two populations: their origin population (i.e., their natal or donor population) and their selected breeding population (i.e., the recipient population). While straying is typically considered as a rate or per capita probability (e.g., 3%), it is important to consider the absolute number of strays as well. Strays are always a demographic loss from the donor population. This can be a management concern when the donor population is limited by the number of breeders or there are risks of genetic bottlenecks. More typically, straying by a small proportion of returning adults has relatively limited negative effects on the donor population. This is because salmonids have high fecundity and their population growth rates are resilient to high levels of adult mortality or reduced homing (Ricker 1972; Kareiva et al. 2000; McClure et al. 2003).

Strays are a demographic gain for the recipient population if they contribute to reproduction or contribute to management-related escapement or harvest objectives. Similarly, a small number of strays have few negative effects on large receiving populations, which tend to be genetically and demographically stable (Tessier and Bernatchez 1999; Waples et al. 2001, 2008). Instead, strays into these populations may add to their overall resilience and genetic stability (Araki et al. 2007; Walter et al. 2009).

Strays can have more direct and substantial effects when donor or recipient populations are small (Figure 1). Small populations can be vulnerable to demographic stochasticity, wherein random or episodic adult mortality, reproductive failure, or skewed sex ratios can have large negative effects on population growth (Lande 1993). Such populations are at considerably greater risk of extinction. Furthermore, small populations can be susceptible to Allee effects, where low population density results in reduced population growth rates (Frank and Brickman 2000; Dennis 2002). Therefore, straying from very small donor populations has the potential to be catastrophic if the remaining breeding population drops below some recruitment threshold. Straying into a small recipient population may potentially contribute to recipient population growth and to its fitness and viability. Indeed, this is a fundamental aspect of salmon evolution and metapopulation dynamics (Hill et al. 2002; Hendry et al. 2004; Quinn 2005; Schtickzelle and Quinn 2007). However, the demographic and ecological effects of strays on small populations are not always positive. For example, strays may compete with local fish for redd sites and mates but fail to reproduce, lowering overall productivity. Those that do successfully breed with the recipient population may dilute locally-adapted traits through introgression.

Straying hatchery fish, in particular, can have a variety of negative genetic, ecological, and fitness impacts on wild recipient populations. These include competitive interactions, displacement, reduced productivity, reduced resiliency, hybridization and domestication effects, and outbreeding depression (Chilcote et al. 1986, 2011; McGinnity et al. 1997; Fleming et al. 2000; McLean et al. 2003; Vasemägi et al. 2005; Williamson et al. 2010; Hess et al. 2011; Johnson et al. 2012). In many salmon- and steelhead-producing regions around the world, strays from large donor hatchery populations are a significant threat to recipient wild populations

(Waples 1991; Fleming and Gross 1993; Quinn 1993; Utter 1998; Reisenbichler and Rubin 1999; Levin et al. 2001; McGinnity et al. 2003; Brenner et al. 2012; Zhivotovsky et al. 2012).

The size of the recipient population relative to the donor population is critically important to understanding potential effects – both positive and negative – of straying. In Figure 1, we used a simple numerical model to demonstrate how straying from a range of donor population sizes affects the demographics of small- to medium-sized recipient populations. Even low (~1%) rates of straying from large donor populations can numerically swamp a small recipient population. Consider, for example, a hypothetical recipient population of 500 natal-origin adults that receives strays from a donor population of 50,000 fish. With a donor straying rate of 1%, the receiving

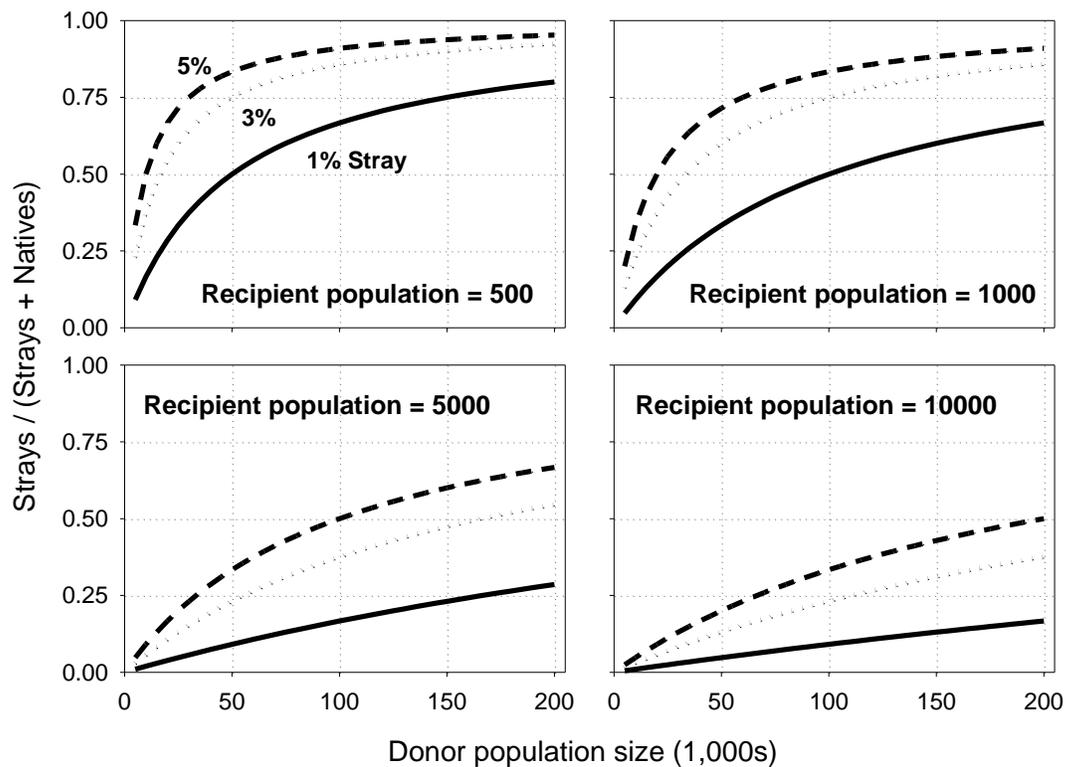


Figure 1. Examples of the proportions of adult strays that spawn with a local recipient population (strays/(strays+natives)) as estimated using four recipient population sizes (four panels: 500, 1,000, 5,000, or 10,000 fish), a range of donor population size (0-200,000), and three donor stray rates: 1% (solid line), 3% (dotted line), and 5% (dashed line). Small recipient populations can be numerically dominated by strays when the donor population is large, even when stray rates are low.

population becomes 500 local fish plus 500 strays, (i.e., 50% strays; Figure 1). When the donor population contributes strays at higher rates or the donor population size increases, strays can rapidly become a majority in the recipient population (Figure 1). All else being equal, these effects would be reduced as the recipient population abundance increases. Importantly, the biological and genetic impacts of strays may be substantial at low relative abundance (e.g., a population where 10% of the breeders are strays may have substantial introgression).

The simple numerical relationships shown in Figure 1 are a simplification of the complex processes that affect breeding and reproductive success. However, they do demonstrate the potential vulnerability of small receiving populations and the management challenge associated with straying by undesirable populations (i.e., hatchery fish). This context is critically important for considering management alternatives related to straying by barged Snake River fish.

3.0 HOMING MECHANISMS

3.1 ROLE OF GENETICS

Successful homing requires migration to the natal location at the appropriate time. Migration timing (Hess and Narum 2011; Quinn et al. 2011), maturation timing (Hendry and Day 2005), and reach-scale homing (Bams 1976; McIsaac and Quinn 1988; Labelle 1992; Bentzen et al. 2001) have all been shown to be heritable traits in anadromous salmonids. However, the specific genes and genetic processes involved are only partially understood. Several genetic mechanisms are potentially important, including control over imprinting and olfaction (Hino et al. 2007, 2009), memory formation and recall, maturation, and senescence (among others).

Several studies have directly or indirectly addressed the genetics of homing. This research has often occurred in the context of management actions, including hatchery production, transplant projects, reintroductions, or efforts to establish new populations. An experiment using hatchery Chinook salmon by Hard and Heard (1999), for example, showed lower homing by adult fish whose parents' gametes had been transported to the hatchery than for fish whose parents had volitionally returned to the hatchery, suggesting a genetic effect. Another circumstantial case study was Candy and Beacham (2000), which showed that stray rates for a hybrid Chinook salmon population (i.e., a cross between stocks) were three times higher than straying by the natal population released at the same location. The same study showed that transplanted fish were more likely to stray to their ancestral river (despite never being exposed to the ancestral site) than control groups. Likewise, Gilk et al. (2004) showed that hybrid pink salmon strayed more than non-hybrids. A broadly similar series of studies on hatchery Chinook salmon in the Columbia River also provided indirect support for a genetic component to homing. McIsaac and Quinn (1988) and Pascual and Quinn (1994) showed that adult Chinook salmon derived from juveniles reared in lower Columbia River hatcheries returned to their ancestral spawning areas (the Hanford Reach) and other upriver sites despite never having been exposed to the ancestral site.

Other studies have examined genetic data to identify the source of pre-spawn adults (e.g., Vasemägi et al. 2005) or to infer the level of inter-breeding between local populations and strays. Tallman and Healey (1994), for example, found that genetic markers indicated lower straying rates than mark-recapture studies of chum salmon. In a genetic study of Klickitat River steelhead, Narum et al. (2006b) concluded that out-of-basin strays likely had lower reproductive success than local populations. Both of these examples suggest that some strays either fail to breed with local populations or have lower overall reproductive success when they interbreed. A genetic marker indicating a predisposition for homing versus straying has not been identified.

3.2 ROLE OF PHYSIOLOGY AND BEHAVIOR

Homing and straying ultimately depend upon a series of physiological and neurological processes in response to developmental and environmental cues across the life cycle. Events that occur during incubation, larval, and juvenile life stages are as important for homing as adult physiology and behavior. There is extensive literature on the various physiological components

of homing. For juveniles, these include cellular-level studies of imprinting in early life stages, studies of stress responses and the endocrine system during early development, physiochemical changes associated with the transition from freshwater to salt water (parr-smolt transformation), and memory development and retention. At the adult stage, homing research has focused on olfactory processes, physiological changes tied to maturation and senescence, memory recall, and orientation behaviors. The latter include rheotaxis, chemotaxis, and proximate responses to other environmental and social cues. These topics are addressed in the following sections.

3.3 JUVENILE IMPRINTING

Two competing hypotheses arose during the early research on salmon homing and each included olfaction (Brannon 1982). One was that adult fish could locate natal sites by responding to pheromones released by juvenile conspecifics at the natal site and along the migration route (Nordeng 1971, 1977; Solomon 1973). The competing hypothesis was that juvenile fish imprinted on unique chemical characteristics (i.e., environmental odors) in water at their natal site and locations during downstream outmigration, and then returning adults used these odors to home (Hasler and Wisby 1951; Wisby and Hasler 1954; Harden Jones 1968). After several decades of laboratory and field experiments, olfactory imprinting is now the consensus homing mechanism used by anadromous salmonids (see reviews by Leggett 1977; Hasler and Scholz 1983; Dittman and Quinn 1996; Nevitt and Dittman 1999; Hino et al. 2009; Ueda 2011, 2012). Importantly, stream odors used for imprinting may include chemicals released by conspecifics or related individuals (i.e., hormones, pheromones), and recognition of such odors has been well documented (Groot

Box 3: Glossary of imprinting and olfaction

- **Amino acids:** carbon-based organic molecules, often complex; dissolve in water; detectable by olfaction
- **β-phenylethyl alcohol (PEA):** artificial odor used in imprinting studies
- **Bile acids / Bile salts:** steroids stored in gall bladder; detectable by olfaction when excreted
- **Chemoreception:** process (i.e., smell, taste) by which animals perceive and respond to external chemical stimuli
- **Epithelium:** tissue associated with secretion, absorption, sensation, and substance transport across cells
- **Guanylyl cyclase:** enzyme in the olfactory system that may facilitate odor recognition, olfactory learning
- **L-serine / L-proline / L-glutamic acid:** amino acids
- **Morpholine:** artificial odor used in imprinting studies; a carbon-based compound
- **Neurotransmitters:** chemicals released by neurons to regulate specific physiological activities
- **Olfactory bulb:** brain structure at terminus of olfactory nerve; transmits information from nose to brain
- **Olfactory imprinting:** unconditioned learning whereby olfactory information is acquired, then used later in life
- **Olfactory receptors:** responsible for detection of odor molecules, starting signal sequence to brain
- **Peripheral memory:** information/memory stored away from the brain, as in olfactory receptor cells
- **Pheromone:** chemical that triggers a behavioral or physiological response in conspecifics when released (i.e., alarm, reproduction, migration, feeding)
- **Pituitary:** endocrine gland that controls many processes, including thyroid gland function
- **Thyroxine / T₄ / T₃:** hormones produced by thyroid gland; associated with stress, smoltification, migration and olfactory imprinting
- **Vomer nasal organ:** contains sensory neurons that detect chemical stimuli, particularly pheromones

et al. 1986; Moore and Scott 1991; Courtenay et al. 1997, 2001).

3.3.1 WHAT ODORS ARE USED FOR IMPRINTING?

Combinations of organic and inorganic materials produce complex chemical signatures in streams and other aquatic systems that can be unique at very fine spatial scales. The homing literature has frequently referred to these signatures as ‘odor bouquets’ and many researchers have worked to identify the specific chemical components that are used by salmonids for imprinting and home site recognition. Candidate source materials have included: bile acids, prostaglandins, pheromones, skin mucus, amino acids, microbes, biofilms, inorganic cations, geologic signatures, soils, stream sediment, aquatic and terrestrial vegetation, and others (Groot et al. 1986; Dickhoff and Sullivan 1987; Quinn 2005). Some of the most recent research using electrophysiological and molecular methods has shown that salmon have high olfactory sensitivity to amino acids (Carruth et al. 2002; Yamamoto et al. 2010; Johnstone et al. 2011; Ueda 2011). These organic, carbon-based molecules are the building blocks for proteins and are present in dissolved organic matter in all types of water. Amino acids can be linked together to form a vast array of proteins, remain stable in their composition, and appear to be the primary imprinting candidate.

3.3.2 WHEN DOES IMPRINTING OCCUR?

Imprinting has been most associated with the developmental stage called the parr-smolt transformation (Hasler and Scholz 1983; Nevitt et al. 1994; Dittman et al. 1996, 1997). Physiological and neurological changes during this stage have been linked to elevated olfactory sensitivity (see Section 3.4 for details). However, sensitive periods differ among species and populations depending on life history and behavior. There is considerable evidence of imprinting during multiple early life stages, including by embryos, alevins, fry, and parr (Riddell and Leggett 1981; Dickhoff and Sullivan 1987; Courtenay 1989; Dittman and Quinn 1996). In fact, pre-smolt imprinting is essential for populations whose juveniles move rapidly to saltwater following emergence (e.g., some chum and pink salmon; Heard 1996) and for populations that rear at locations downstream from spawning sites (e.g., sockeye salmon that spawn in tributaries to rearing lakes). Chinook salmon, coho salmon and steelhead vary in the spatial extent of freshwater rearing with some populations rearing very close to natal sites to well downstream in more productive habitats (Peterson 1982; Groot and Margolis 1991; Connor et al. 2001; Brannon et al. 2004). This diversity suggests that imprinting time is a relatively plastic trait and is likely episodic for many species and populations (Figure 2). In other words, imprinting can occur at natal sites, rearing sites, at other sites along migration routes, and in response to proximate stimuli, though the strength of imprinting varies through time.

3.3.3 MULTIPLE / SEQUENTIAL IMPRINTING

Imprinting almost certainly happens during active migration, particularly for long-distance migrants and those in complex river systems with many tributary inputs. Multiple imprinting events may also be common for juveniles with extended freshwater residency times and those that move among habitats prior to outmigration. This ‘sequential imprinting’ potentially occurs as juveniles transition through physiological states and when they encounter novel odors

associated with changes in ecological and environmental conditions (Harden Jones 1968; Brannon 1982; Dickhoff et al. 1982). The term is most often applied to imprinting during the course of juvenile outmigration (Figure 3). Imprinting in a series of spatially discrete events along the migration route is hypothesized to provide olfactory waypoints that can be recognized in reverse sequence during adult return migration.

Sequential imprinting is logistically challenging to examine directly. However, studies where juvenile salmonids have been transported various distances do offer some insight on this process. Transport studies of coho salmon (Solazzi et al. 1991) and Atlantic salmon (Gunnerød et al. 1988; Heggberget et al. 1991), for example, have shown that adult homing success is inversely related to juvenile transport distance from rearing sites. Similarly, juvenile salmon and steelhead collected in mid- migration and then transported downstream tend to home at lower rates than control groups that remain in the migration corridor (Hansen and Jonsson 1991; Bugert et al. 1997; Chapman et al. 1997; Keefer et al. 2008b). These patterns suggest that transport results in missed or disrupted imprinting events. In cases where fish are removed from the migration route (i.e., in trucks) there is clearly no imprinting opportunity in the missed segment, and fish transported great distances by truck often have very poor homing. When fish are transported in the river corridor (i.e., in barges), imprinting opportunity may be compromised by temporal effects (i.e., transport is too rapid), spatial effects (i.e., the transport route does not sample the habitats required for successful imprinting), or physiological factors (i.e., transport interferes with imprinting receptivity).

In wild fish, evidence for sequential imprinting is circumstantial but highly likely for populations whose life history results in spatially separated incubation and rearing locations. It is also highly implausible that adults from populations with long freshwater migration distances could detect dilute olfactory signatures from small natal streams far downstream in well-mixed, high volume migration corridors or estuaries (Quinn 2005).

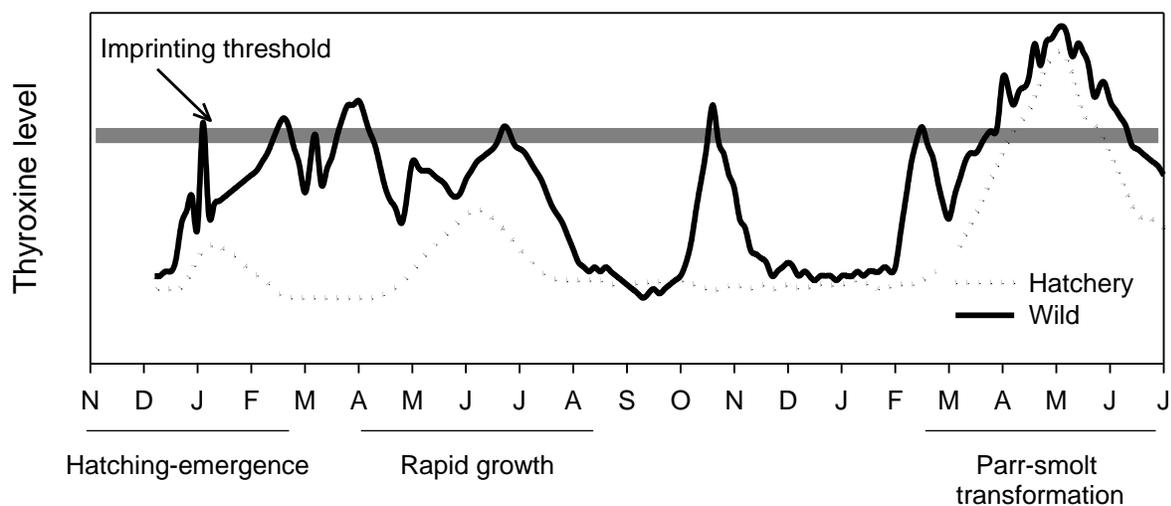


Figure 2. Hypothetical relationship between thyroxine level and the threshold for olfactory imprinting in wild (solid line) and hatchery-reared (dotted line) salmon. Imprinting can occur throughout early life history stages and appears to be episodic in wild populations. Modified from Dittman and Quinn (1996).

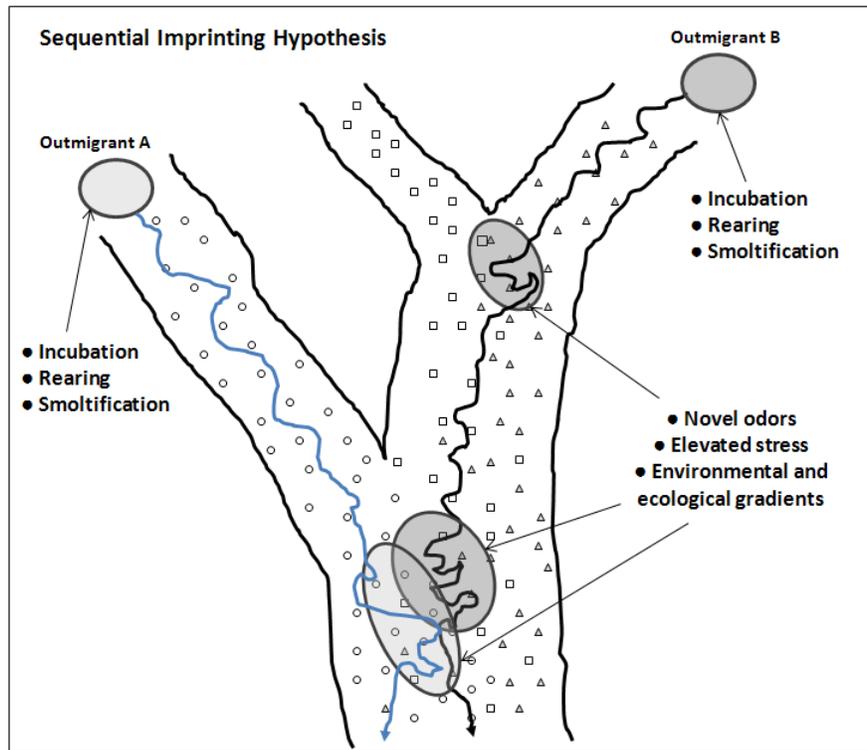


Figure 3. Hypothetical examples of sequential imprinting by juvenile migrants. Olfactory imprinting can occur at and near natal sites, during incubation and rearing and during the parr-smolt transformation. Additional imprinting can occur during outmigration as juveniles encounter novel ecological and environmental conditions as well as new chemical / odor complexes. Elevated hormones and stress responses during migration likely facilitate imprinting at these sites.

3.3.4 HOW DOES IMPRINTING OCCUR?

Olfactory imprinting is a form of unconditioned learning where a stimulus in one life stage has no immediate benefit or response, but rather is used to advantage in a later stage. An array of physiological processes is involved (Dittman et al. 1997; Nevitt and Dittman 1999; Hino et al. 2009; Ueda 2011, 2012). These include hormonal activity controlled by the pituitary system, olfactory processes related to odor detection, the development of receptor neurons in the vomeronasal organ, and the generation of odor-related receptors and 'memories' in the olfactory epithelium (in the nasal cavity) and olfactory bulb (in the brain) (Bargmann 1997). See Box 3 for definitions.

In salmonids, imprinting events are apparently preceded by an increase in hormones produced by the thyroid gland, and particularly by surges in thyroxine (T_4) and triiodothyronine (T_3) (Figure 2). Thyroid hormones affect a variety of processes ranging from metabolic rate and growth to neuron development and maturation. Thyroid hormone surges in juvenile salmonids have been associated with increased sensitivity and cell growth in the olfactory epithelium (the tissue that holds olfactory receptor cells in the nose) and with development of olfactory receptor neurons (Nevitt et al. 1994; Nevitt and Lema 2002; Lema and Nevitt 2004).

Olfactory receptors detect and bind odor molecules such as amino acids or pheromones in a process broadly defined as chemoreception. Once bound, a biochemical process converts the odor signal to an electrical signal that is transmitted to the brain, and specifically to the olfactory bulb where memory is stored (Nevitt and Dittman 1999). Additionally, the receptor neurons in the epithelium proliferate during thyroid surges and the cells themselves survive and remain sensitive to the imprinted chemicals (Dukes et al. 2004). The current understanding, as described by Nevitt, Dittman, and colleagues, is that olfactory imprinting involves memory storage in both the brain and the neural cells in the nasal epithelium. The latter is referred to as ‘peripheral’ memory because it stored outside the brain.

The link between thyroid hormones and imprinting is critical to understanding the timing and degree of imprinting in juvenile salmonids. In wild fish, some of the largest thyroid surges occur during the parr-smolt transformation, but spikes in thyroid activity also occur in fertilized eggs, developing eggs, alevins, fry, and parr (Dickhoff and Sullivan 1987; Power et al. 2001). Furthermore, environmental stimuli ranging from changes in temperature and flow to lunar cycles affect thyroid production (Lema and Nevitt 2004). In the wild, changing environmental conditions and stress promote frequent hormonal fluctuations (Figure 2), which in turn generate olfactory receptor neurons and imprinting opportunities. In contrast, juveniles reared in relatively stable hatchery environments show fewer and lower amplitude hormone surges. These differences likely explain the reduced imprinting and an apparently greater propensity for straying in hatchery versus wild salmonids (Nishioka et al. 1985; Dittman and Quinn 1996; Björnsson et al. 2011).

The olfactory processes described in this section are genetically controlled, at least in part, by olfactory receptor genes (Dukes et al. 2004; Hino et al. 2009). Johnstone et al. (2011) recently showed that olfactory genes are expressed differently among parr, smolts, and adults in Atlantic salmon with an anadromous life history. In contrast, a landlocked population showed no differences in which olfactory genes were expressed in the different life stages. The authors concluded that regulation of these genes is linked to physiological state (i.e., parr-smolt transformation) and to environmental cues. Whereas the anadromous populations must activate specific receptor cells to imprint on natal waters, prepare for saltwater entry, and recall the home stream odors as adults, the life history of landlocked salmon does not appear to require these processes and hence these genes are not upregulated. We note that olfaction is used for homing migration in a variety of non-anadromous species but that the genetic regulation of these processes is not well understood.

3.3.5 IMPRINTING EXPERIMENTS

Evidence supporting the role of olfaction in homing accumulated over an extended period starting in the 1950s. An influential first experiment by Hasler and Wisby (1951) demonstrated that odor-conditioned bluntnose minnows (*Pimephales notatus*) used olfaction to learn and later differentiate water from two Wisconsin creeks. The same experiment showed that the chemical signature recognized by the study fish was stable through time, which was an important requirement for homing salmonids given their years away from the natal site.

Hasler and his students then embarked on a series of imprinting experiments using artificial odorants and coho salmon. They exposed juvenile salmon to the organic compounds morpholine or β -phenylethyl alcohol (PEA, Box 3) and then tested whether returning adults could be attracted to water sources with these chemicals (Wisby and Hasler 1954; Hasler 1966; Cooper et al. 1976; Scholz et al. 1976). Olfactory occlusion (i.e., plugged nasal sacs) and blinding was used on some adults to confirm the role of odor detection in the homing behaviors. Variations on this experimental approach were subsequently applied to other species and in different river systems, with consistent support for the imprinting hypothesis (reviews in Hasler 1966; Hasler et al. 1978). By the late 1970s, the general consensus was that juvenile salmonids imprint on persistent chemicals unique to their home stream, retain the imprinted information through adulthood, and then use the same chemicals during homeward migration.

During this same era, physiological experiments tested the sensitivity of olfactory cells to both the artificial odorants used in imprinting studies and to natal stream waters (Hara et al. 1965; Ueda et al. 1967; Cooper and Hasler 1976). Other research examined the relationship between hormones (e.g., thyroxine) and imprinting and concluded that the most sensitive period was the parr-smolt transformation when thyroid hormones were elevated (Hasler and Scholz 1983; Morin et al. 1989, 1992, 1994; Dittman et al. 1996). Experiments using earlier life stages also showed that embryos, alevins and fry exposed to specific odorants would respond to those same chemicals several months later as parr (Dickhoff and Sullivan 1987; Courtenay 1989) though not necessarily as adults (Dittman et al. 1996). Importantly, the observation of weak response in adults in the experiments was at least partially an artifact of using hatchery fish, which have lower hormonal fluctuations. A more field-based study of hatchery Chinook salmon in New Zealand during this era suggested that imprinting by fry to the natal tributary was distinct from imprinting by smolts in the main stem river (Unwin and Quinn 1993).

More recent neurobiological experiments using electrophysiology and molecular techniques have demonstrated that salmon can imprint on single amino acids present in their home stream water. For example,

Box 4: Glossary of parr-smolt physiology

- **ATPase:** Shorthand for Na^+ , K^+ -adenosine triphosphatase, an enzyme that helps gills regulate ions and the transition from fresh to salt water; associated with active migration and elevated imprinting
- **Chronic stress:** repeated or long duration (i.e., weeks-months); can slow parr-smolt transformation and suppress a variety of physiological functions
- **Cortisol / Corticosteroids:** produced by adrenal gland, these hormones inhibit immune function but stimulate ATPase production and indirectly facilitate imprinting
- **Endocrine system:** glands that secrete hormones into the bloodstream, including adrenal, pituitary, and thyroid
- **Growth hormones:** produced by pituitary gland; help mobilize stored energy
- **Ionoregulation:** regulation of ion concentrations in body fluids; critical for the transition to salt water
- **Osmoregulation:** regulation of osmotic pressure / water content / excretion / salinity
- **Parr-smolt transformation (PST):** shorthand for the physiological, morphological and behavioral changes needed for transition to saltwater
- **Plasma chloride:** a blood-based stress indicator and measure of ionoregulatory response
- **Thyroxine / T4 / T3:** hormones produced by thyroid gland; associated with stress, smoltification, migration and olfactory imprinting

sockeye and chum salmon exposed to L-proline and L-glutamic acid during the parr-smolt transformation preferentially recognized those amino acids as adults (Yamamoto et al. 2010; Bando et al. 2011). Longer exposure periods resulted in stronger imprinting, and brain imaging showed that adult recognition of the home stream amino acids was associated with activity in the olfactory bulb.

3.4 ROLE OF PARR-SMOLT TRANSFORMATION AND OUTMIGRATION

The parr-smolt transformation (PST, synonymously referred to as ‘smoltification’) is a hormone-driven developmental process that is cued by environmental change and especially by photoperiod and water temperature (Zaug and Wagner 1973; Hoar 1988; McCormick et al. 1987, 1998). Briefly, smolting prepares juveniles for downstream migration and ocean residency via increased salinity tolerance (i.e., changes in ionoregulatory and osmoregulatory function), increased metabolism, changes in behavior (i.e., schooling, negative rheotaxis), and changes in appearance (i.e., body shape and color). These processes are largely controlled by a suite of hormonal surges, including insulin and growth hormones, cortisol and other stress hormones, and thyroid hormones (Beckman et al. 2003; Quinn 2005; McCormick 2009; Björnsson et al. 2011).

Many parallel processes are at play during the PST, and it can be difficult to separate cause and effect with regards to imprinting. It is clear, however, that the suite of physiological changes associated with migration and preparation for saltwater entry are intimately linked to olfaction and memory. The thyroid hormones associated with imprinting (see Figure 2), for example, also influence morphological and pigmentation changes and the development of salinity tolerance in smolts (Dickhoff et al. 1978; Hoar 1988; McCormick et al. 1998). Simultaneously, increases in the stress hormone cortisol affect production of $\text{Na}^+\text{K}^+\text{ATPase}$ in the gills. Levels of ATPase enzymes are strongly associated with the timing of migration and saltwater entry, and have therefore been used as an indicator of imprinting readiness (Slatick 1988). Concurrent increases in growth hormones tend to accelerate the physiological changes of smoltification (McCormick et al. 2009).

Importantly, the act of migration itself stimulates hormone production. In particular, thyroid and adrenal hormones tend to spike as smolts encounter new environmental, ecological, and chemical stimuli. Behavioral changes, including the shift from positive to negative rheotaxis, are also mediated by the anatomical and physiological changes. These multiple feedback loops tied to outmigration strongly reinforce the association between PST and imprinting. In fact, interrupting or preventing migration has been shown to negatively affect imprinting. There are several examples of reduced adult homing when smolts were held in a hatchery during the PST (i.e., smolt migration was inhibited; Hansen and Jonsson 1991; Unwin and Quinn 1993; Dittman et al. 1996). These patterns suggest that preventing volitional downstream smolt migration negatively affects imprinting even when the smolts experience relatively normal hormonal and physiological development while held.

3.5 ROLE OF HATCHERY REARING

As mentioned in previous sections, hatchery-reared salmon and steelhead experience different environmental conditions than wild fish, resulting in divergent physiological and developmental

trajectories for the two groups (Dittman and Quinn 1996; Congleton et al. 2000). Wild fish rearing in dynamic environments appear to have a more flexible and opportunistic imprinting system than fish reared in the relatively stable environments found in most hatcheries (i.e., low structural complexity, limited predators, ample food, constant flow rates, and fewer temperature extremes). Hatchery fish consistently have lower growth and thyroid hormones, lower ATPase, and lower cortisol levels and gill cortisol receptors than closely related wild-reared fish (Virtanen and Soivio 1985; Shrimpton et al. 1994; Sundell et al. 1998; McCormick et al. 2003; Chittenden et al. 2008). Hatchery effects also shape neural and brain development (Marchetti and Nevitt 2003), and the combined effects result in reduced imprinting.

In their review of smoltification, Björnsson et al. (2011) concluded that the intensity of many hormonal and physiological processes is reduced in hatchery fish. The dampening of endocrine signals results in fewer imprinting opportunities inside the hatchery (see Figure 2). Depending on release timing (i.e., as parr, pre-smolt, smolt, or post-smolt), hatchery-reared fish have varying lengths of time to imprint on waters near the release site. Fish released as pre-smolts may have the most opportunity for local imprinting because they are exposed earlier to natural environmental fluctuations and are less likely to immediately emigrate. Such releases are relatively uncommon, however, because hatchery managers try to minimize juvenile freshwater residency and mortality. Both parr and smolts experience increased thyroxine levels after hatchery release, whereas smolts but not parr also have increased growth hormone and ATPase (McCormick et al. 2003). These changes are not necessarily in synchrony with wild fish in the same system, however, particularly when incubation or rearing schedules in the hatchery are markedly different from those in the receiving system. Lastly, the relatively common practice of releasing hatchery fish in mid- or late-PST may result in rapid downstream movement and potentially reduced imprinting near the release site.

Hatchery salmon and steelhead have been used in the vast majority of juvenile imprinting studies. As described above, however, juvenile hatchery fish are physiologically compromised when compared to their wild counterparts and this has complicated interpretation of study results, particularly for extrapolating to wild fish. As will be discussed in the following sections, much of the adult homing and straying research has also relied on hatchery fish. Disentangling the effects of hatchery rearing from other mechanisms associated with imprinting, homing, and straying continues to be a critical challenge in the field.

3.6 ADULT HOMING

The remarkable adult migrations of salmon and steelhead can cover thousands of kilometers from distant ocean feeding areas, through coastal and estuarine waters, and then through a variety of freshwater environments to their natal sites. Ocean distributions and homeward migration routes and distances differ widely among species and populations, and migrants appear to use a variety of navigation and orientation mechanisms. In the ocean portion, navigation may include the use of bi-coordinate map or compass systems such as polarized light, magnetic fields, or celestial compasses (Neave 1964; Døving et al. 1985; Quinn 1990, 2005; Pascual and Quinn 1991; Hansen et al. 1993; Dat et al. 1995; Bracis and Anderson 2012). Salmon may navigate using these same mechanisms in the near-shore ocean and in estuaries, along with orientation by

visual and olfactory cues, plus environmental cues from currents, salinity, water temperature, and freshwater inputs from rivers.

It is not known which combinations of orientation and navigation systems salmonids use or the degree to which they vary along migration routes or among species. Furthermore, while it is clear that olfaction is a dominant orientation mechanism in late stages of freshwater migration (i.e., while approaching the natal site), the point at which adults switch to primarily olfaction from other orientation systems is also unknown. (Note: While orientation and navigation in salt water is critically important for understanding large-scale homing behaviors, there has been limited homing research in the oceans and it is beyond the scope of this review. In the following sections, we focus on adult homing during the freshwater phase of migration.)

3.6.1 ADULT HOMING MIGRATION PHYSIOLOGY

Adult salmonids go through significant physiological changes during homing migration. These include a reversal of the osmoregulatory and ionoregulatory changes experienced by smolts during the transition into salt water, increases in reproductive hormones (e.g., testosterone, estradiol, gonadotropin, etc.) associated with maturation, and changes in color and morphology via development of secondary sexual characteristics (Hendry and Berg 1999; Groot and Margolis 1995; Ueda 2011). Semelparous species also begin to senesce, typically starting with the cessation of feeding and including impaired immune function and the degeneration of most organs and the central nervous system (Carruth et al. 2002; Morbey et al. 2005).

Adult migration and senescence also feature a surge in stress hormones, particularly cortisol and other glucocorticoids, which often peaks during migration, declines during spawning, and then increases again prior to death (Dickhoff 1989; Carruth et al. 2000). Stress hormones can impair learning and

Box 5: Glossary of adult homing migration

- **Chemotaxis:** orientation towards chemical cues, including olfactory cues
- **Cortisol:** stress hormone that controls an array of functions; associated with increased olfactory sensitivity in maturing salmonids
- **Estradiol:** estrogen hormone affecting reproductive functions and secondary sexual traits
- **Glucocorticoids:** group of steroid hormones that includes cortisol; affect immune system and metabolism
- **Gonadotropin:** pituitary hormone that controls growth, sexual development, and reproductive function
- **Guanylyl cyclase:** olfactory enzyme associated with odor recognition; maturing salmon show increased g-c sensitivity and it likely facilitates salmon homing
- **Navigation:** ability to move from one location to another (i.e., homing) without prior information about the route; requires sense of direction and geographic position
- **Odor-conditioned rheotaxis:** when animals use a combination of olfactory and rheotactic cues during movement; likely used for homing in complex environments
- **Orientation:** moving towards a stimulus, such as light, food, or odor; the physiological basis for navigation
- **Rheotaxis:** innate behavior where fish orient into the current (positive rheotaxis) or orient away from current (negative rheotaxis)
- **Senescence:** rapid aging that includes decline in immune function, organ and cell atrophy, starvation, and elevated stress hormones; associated with maturation and post-reproduction death in semelparous salmonids

short-term memory, but they serve a variety of useful functions for maturing adults. In regards to homing, stress hormones have been shown to enhance long-term memory recall. Carruth et al. (2002) describe how, in sexually maturing salmon, neurons that bind glucocorticoid hormones are present in several regions of the brain that are involved in olfaction. This suggests that stress hormones in adults are important for stimulating olfactory processes and likely have an adaptive role in the recall of imprinted odors.

The enhanced olfactory sensitivity of adult salmon during homing migration has also been linked to the reproductive hormone gonadotropin (Fitzpatrick et al. 1986) and to the enzyme guanylyl cyclase (Dittman et al. 1997). Gonadotropin plays a role in gonad maturation but levels of this hormone have also been shown to increase in the olfactory bulb and other olfactory-related brain regions during homing migration (Hasler and Scholz 1983; Ueda and Yamauchi 1995; Ueda 2011). Guanylyl cyclase is a chemoreceptor that is active in the olfactory system whose sensitivity level increases during salmon maturation and prior to spawning. The relationship between reproductive maturity and recognition of imprinted odors has been experimentally demonstrated, with limited behavioral response to home stream odors (or artificial odorants) by non-ripe adults prior to spawning compared to mature adults (Cooper and Hasler 1973; Hasler and Scholz 1983; Dittman et al. 1996).

Iteroparous species experience essentially the same reproductive maturation processes as semelparous species, but senescence is regulated differently in individuals that survive post-spawning. Senescence in repeat spawners, or the lack thereof, may be genetically controlled or be associated with age, number of spawning events, migration distance, or some combination of factors (Crespi and Teo 2002; Keefer et al. 2008d). Cortisol appears to play an important role in determining whether iteroparous individuals survive or die, with much higher levels of cortisol and related stress hormones in those that die (Barry et al. 2005).

The inter-relationships between homing migration, maturation physiology, and olfactory sensitivity are not fully understood. For example, many populations migrate long distances in freshwater and then hold for weeks to months before fully maturing (Berman and Quinn 1991; Hansen and Jonsson 1991; Økland et al. 2001; Hodgson and Quinn 2002). This is especially pronounced in summer-run steelhead, which often initiate their homing migration 6-10 months prior to spawning and can hold for months at sites distant from natal areas (Busby et al. 1996; High et al. 2006; Keefer et al. 2008c, 2009). Lower levels of reproductive hormones for 'early' migrants (like steelhead) that enter freshwater well before maturation suggest that they may have reduced olfactory sensitivity compared to those with more advanced maturation schedules. It is also possible that pre-spawn holding downstream from natal areas includes waiting for olfactory sensitization.

3.6.2 ADULT HOMING BEHAVIOR: MIGRATION CORRIDORS

Adult salmonids primarily rely upon rheotactic and olfactory cues during upstream migration, a combination that is widely used by aquatic species and is commonly referred to as odor-conditioned rheotaxis (Zimmer-Faust et al. 1995; Weissburg 2000; Carton and Montgomery 2003). In the salmonid literature, Johnsen (1982), Quinn (2005), and DeBose and Nevitt (2008) have most explicitly described this orientation strategy in reference to homing. They propose

that adults orient into the current (positive rheotaxis) and proceed upstream with limited lateral movement when familiar odors are present (Figure 4). When the expected olfactory cues are diffuse or mixed, the fish include lateral searching or upstream zigzagging along odor plumes created by tributary inputs, thermal layers, or other physiochemical gradients. When home stream odors are absent, the fish retreat downstream until the cue is relocated. When home stream odors are absent, the fish retreat downstream until the cue is relocated.

In deep or stratified riverine habitats, including reservoirs, odor-conditioned rheotaxis can include vertical searching movements. Døving et al. (1985) showed that adult Atlantic salmon make frequent vertical movements in fjords with stratified water layers. This behavior was positively related to olfaction by testing the response of the salmon's olfactory neurons to different water layers, and later by experiments with anosmic (i.e., no olfactory function) fish (Døving and Stabell 2003). In rivers and estuaries, similar frequent but short-duration vertical movements have been reported for several species (Westerberg 1984; Olson and Quinn 1993; Johnson et al. 2005, 2010), and these behaviors presumably also facilitate olfactory sampling.

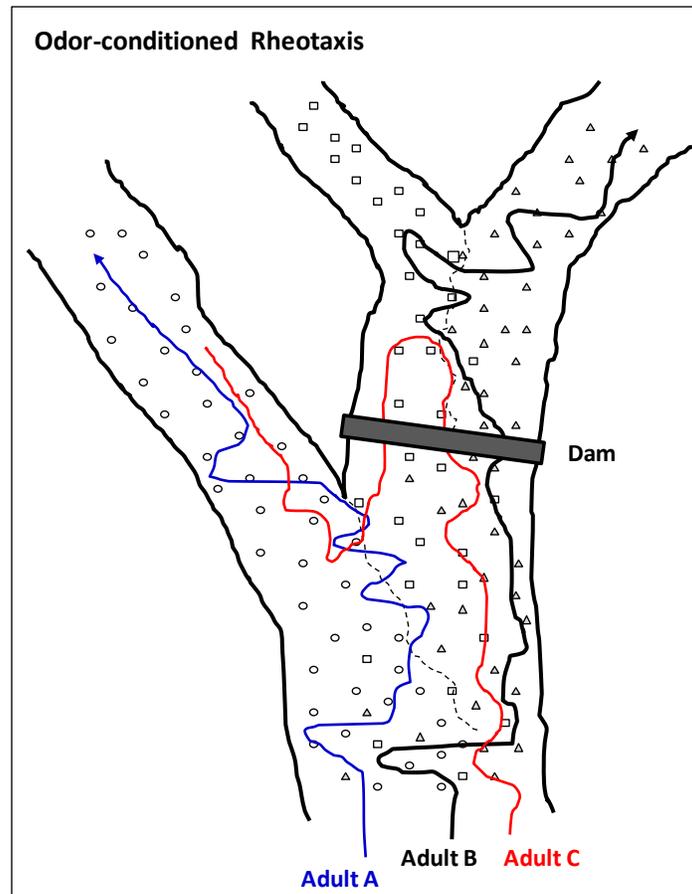


Figure 4. Hypothetical examples of odor-conditioned rheotaxis by homing adult migrants where the open symbols represent odor signals from three tributaries and the lines represent migration routes. Upstream migrants move more directly upstream when both rheotactic and familiar olfactory cues are clearly present. When the olfactory cue is absent, migrants move laterally (examples A & B) or retreat downstream (examples B & C) until the cue is relocated. They then resume upstream movement. Example B is representative of 'testing' or 'temporary straying' behavior, while example C demonstrates natal tributary overshoot and dam fallback. Modified from Johnsen (1982) and DeBose and Nevitt (2008).

Evidence for odor-conditioned rheotaxis at relatively large spatial scales in freshwater has been inferred from the behavior of radio-tagged adult Chinook salmon and steelhead in the Columbia River. Dams and reservoirs on the Columbia River have altered the olfactory landscape for adult migrants, by increasing the cross section of the river channel, turbulent mixing in some locations (i.e., from spillways and turbines), odor diffusion, increased cohesion of tributary plumes in reservoirs in some locations, and the disruption of plumes from tributaries in locations near dams (e.g., John Day Dam and River). Despite these effects, Chinook salmon migrating in the lower Columbia River migration corridor preferentially orient to the shoreline where their natal river enters the main stem (Keefer et al. 2006a). Many migrants initiate this preference tens to hundreds of kilometers downstream from their natal tributary confluence with the Columbia River, apparently by distinguishing lateral gradients in olfactory or other cues. Chapman et al. (1997) similarly reported that tagged Columbia River sockeye and Chinook salmon preferentially migrated along Columbia River shorelines with stronger cues from natal areas.

Evidence for impaired odor-conditioned orientation in the Columbia and Snake River main stems is supported by frequent ‘overshoot’ of natal tributaries and by extensive up- and down-stream wandering by tagged salmon prior to natal tributary entry (Bugert et al. 1997; Hayes and Carmichael 2002; Boggs et al. 2004; Keefer et al. 2006b, 2008a, 2008b; Bumgarner and Dedloff 2011; Gallinat and Ross 2011). Columbia River populations with relatively high documented overshoot rates include John Day, Umatilla and Walla Walla River stocks in the lower-mid Columbia River, Hanford Reach stocks in the upper-Columbia, and Lyons Ferry Hatchery and Tucannon River stocks in the lower Snake River. Overshoot distances can be considerable in the Columbia system (i.e., > 200 km upstream), but are more typically in the range of 10’s of kilometers. Overshoot behavior often includes passage of main stem dams upstream from the natal site, resulting in volitional fallback downstream over dams as migrants attempt to relocate olfactory cues from their natal river (Figure 4).

In less regulated rivers, overshoot behaviors by adult salmonids have also been reported on the scale of 10’s of kilometers and typically occur relatively close to spawning areas (Heggberget et al. 1988; Thorstad et al. 1998; Økland et al. 2001).

3.6.3 ADULT HOMING BEHAVIOR: EXPLORATION AND TESTING

Exploration of non-natal habitats appears to be to be an innate part of adult salmon and steelhead breeding behavior. There are many examples of adults ‘testing’ novel habitats during migration or while actively searching for spawning sites and mates (Burger et al. 1995; Økland et al. 2001; Anderson and Quinn 2007; Keefer et al. 2008a). Some of this behavior occurs at sites that are distant from natal areas in response to environmental cues (Goneia et al. 2006; Keefer et al. 2008a, 2009; Clarke et al. 2010, 2011). More commonly, testing and proving behaviors have been observed at sites near spawning grounds, and typically include movements that range from hundreds of meters to 10’s of kilometers (Burger et al. 1995; Griffith et al. 1999; Økland et al. 2006; Connor and Garcia 2006). Males appear to be more likely than females to move among potential spawning sites as they search for mates (Hard and Heard 1999; Keefer et al. 2006; Neville et al. 2006; Anderson and Quinn 2007; Hamann and Kennedy 2012). Importantly, the relationship between exploration and permanent straying is unclear (see Section 4.1.4). It is also unknown whether some individuals are genetically predisposed to test novel habitats (the

observation of higher rates of movements in males suggests some genetic control) or whether ecological context is the primary trigger for these types of behaviors.

4.0 ADULT STRAYING

4.1 DEVELOPING A STRAYING LEXICON

Quantifying adult salmon and steelhead straying behavior is difficult for several reasons. Among the most significant practical challenges are identifying appropriate spatial scale(s), distinguishing straying fish from homing fish, and the incomplete census of potential straying locations. A second set of challenges stem from the terminology used to describe homing- and straying-related behaviors. First, the straying literature does not always clearly distinguish between straying estimates based on donor populations (i.e., how many fish stray *from* a site or population) versus estimates based on receiving populations (i.e., how many stray *into* a site or population). These two perspectives have very different ecological and management implications. Second, many behaviors exhibited by adults during homing migration have elements of straying, but result in successful homing. These include exploration and testing of non-natal waters, searching for mates, pre-spawn holding, and use of non-natal sites in response to social or environmental cues (e.g., behavioral thermoregulation). Fish with these behaviors are often captured at hatchery traps and weirs or in fisheries in non-natal areas, and their homing versus straying status is therefore ambiguous.

4.1.1 THE CHALLENGE OF SPATIAL SCALE

Straying is fundamentally a spatial question, but the distinction between fish that successfully home and those that stray is often far from clear cut. There are important differences in the spatial structuring among species and among populations that need to be factored into any straying assessment. Genetically and phenotypically distinct populations can evolve in very close proximity, occasionally even sharing the same spawning sites but with temporal separation that limits inter-breeding (e.g., Bentzen et al. 2001; Hendry 2001; Stewart et al. 2003; Quinn et al. 2006, 2012; Narum et al. 2007; Lin et al. 2008). For populations with very fine-scale spatial structuring – at the scale of specific stream reaches or spawning beaches – fish that spawn 100's of meters or a few kilometers away from their natal sites could be considered strays, though such populations are rarely managed as separate groups.

Many other populations appear to home at the sub-watershed scale (i.e., to specific tributaries within a larger drainage) or to habitat complexes (i.e., to a region with many spatially discrete spawning sites but similar habitat features and olfactory landscapes). Straying from these populations may require movements away from natal sites of kilometers to 10's of kilometers (or more). Conclusively differentiating homing fish from strays in populations with meso-scale spatial structuring requires information on the genetic relatedness of different spawning aggregations as well as an understanding of how spawner distribution and habitat varies through time (e.g., Quinn 2005; Narum et al. 2006a, 2006b, 2008; Dittman et al. 2010; Hamann and Kennedy 2012; Peacock and Holt 2012). Identifying local and meso-scale straying can be particularly difficult when there is limited genetic differentiation or weak sub-population structuring within a spawning aggregate (Neville et al. 2006; Lin et al. 2011).

There is generally less ambiguity about classifying strays as the spatial scale increases because the likelihood of breeding with genetically-unrelated fish typically increases with distance. This

clearly occurs when fish spawn in lower versus upper tributaries of large watersheds (Unwin and Quinn 1993; Keefer et al. 2005) and when they spawn in geographically distant river systems (e.g., Labelle 1992; Unwin and Quinn 1993; Jonsson et al. 2003; Pess 2009).

Defining spatial criteria for identifying straying can be especially difficult for hatchery populations, whose behaviors can be influenced by ancestral source, hybridization, rearing and release strategies, transportation, inter-basin transfers, and a variety of other confounding factors. Unfortunately, the vast majority of straying studies have used hatchery fish, which are often poor analogs for wild populations. It is often unclear what the appropriate criteria should be for identifying strays that reared in one location (i.e., a central hatchery facility) and were then outplanted at one or more satellite locations (e.g., Lirette and Hooton 1988; Candy and Beacham 2000; Schroeder et al. 2001) or were released in the home river, but at different locations along the migration corridor (e.g., Solazzi et al. 1991; Gorsky et al. 2009). Such fish potentially imprint on both the rearing hatchery and the release site, and the spatial proximity of the two clearly affects interpretation of “natal site” and adult distribution. Similarly, it can be difficult to categorize as straying those adults that return to their ancestral site rather than to locations affiliated with their rearing hatchery (e.g., Pascual and Quinn 1994; Brenner et al. 2012).

4.1.2 THE CHALLENGE OF IDENTIFYING STRAYS

There are essentially two methods that have been employed to identify strays: 1) using marks or tags applied to juvenile fish (e.g., coded wire tags, PIT tags, fin clips, thermally induced otolith marks), and 2) using genetic testing or patterns in fish otoliths to infer origin. A challenge shared by all methods is that all possible straying locations are rarely surveyed. Estimates of straying *from* any given population are therefore likely biased because some portion of the adult strays is never detected. Stray recovery efforts are frequently restricted to sites with capture and sorting facilities like hatcheries and weirs. Less frequently, strays are identified during carcass surveys (e.g., Mortensen et al. 2002; Dittman et al. 2010; Ruzycski and Carmichael 2010; Brenner et al. 2012) or in monitored fisheries (e.g., Youngson et al. 1997; Keefer et al. 2005; 2008a; Carmichael and Hoffnagle 2006; Clarke et al. 2010), though again recovery effort varies widely and potential sampling biases are rarely quantified.

An ideal estimate of straying *from* a population requires information on the final distribution of all adults in a single year class or all adults from a single brood-year. This is rarely, if ever, possible. Likewise, an ideal estimate of straying *into* a population requires information on the natal source of all adults at the site. Such estimates are possible when all fish returning to a spawning area are processed (i.e., at a hatchery trap or collection weir) and either the entire homing population is marked or the origins of all fish can be assigned using genetic methods. Sub-sampling techniques may be sufficient if samples are spatially and temporally representative of both the potential strays and the recipient population. There are almost no examples of complete-census straying studies, especially for wild populations.

4.1.3 DONOR VERSUS RECIPIENT POPULATIONS

In our opinion, the straying literature has disproportionately reported on straying rates from donor populations and under-reported on straying into receiving populations. This has been an

artifact, at least in part, of hatchery programs marking juvenile fish and strays being recovered and identified using those marks. The emphasis should perhaps be reversed, as many of the most pressing management and ecological questions related to straying are from the perspective of the receiving population. Good examples of recipient population straying estimates include studies of Atlantic salmon in Iceland (Isaksson et al. 1997), hatchery chum, pink, and sockeye salmon in Alaska (Brenner et al. 2012), hatchery Chinook salmon in the Tucannon River (Milks et al. 2006; Gallinat and Ross 2011), coho salmon in British Columbia (Labelle 1992), steelhead in western Oregon (Schroeder et al. 2001), and steelhead in the John Day and Deschutes River basins (Hand and Olson 2003; Ruzyki and Carmichael 2010). See section 6.5 for details on these studies.

4.1.4 PERMANENT VERSUS ‘TEMPORARY’ STRAYING

Several adult salmon behaviors and human interventions complicate the straying lexicon because they result in some – but not all – of the elements of straying. A simple, biological definition of straying by Quinn (1993) had three elements: 1) migration, 2) spawning, and 3) use of a site other than the natal site. Potential ambiguity in the third element is the appropriate spatial scale for defining natal site homing, which is discussed in Section 4.1.1. The second element (spawning) can also be difficult to classify. With the exceptions of carcass surveys and some telemetry studies, the spawning success or failure of individual strays is often unknown. This is especially true when strays are collected at hatchery traps or weirs and are not allowed to retreat downstream or volitionally select spawning locations (McIsaac and Quinn 1988; Pascual et al. 1995; Griffith et al. 1999; Chapman et al. 1997). Similarly, ‘strays’ identified via capture in fisheries may or may not have spawned at their natal sites had they survived (Keefer et al. 2005; Carmichael and Hoffnagle 2006; Naughton et al. 2009; Clarke et al. 2010, 2011). The first element in the definition (migration) can be complicated by wandering and exploratory movements (Figure 5) and by thermoregulatory behaviors. These behaviors have been collectively – and perhaps inappropriately – referred to as ‘temporary straying’.

In the Columbia River basin, permanent straying by hatchery fish that then breed with wild fish is a pervasive management issue. Of particular concern is straying by hatchery salmon and steelhead from upriver populations into distant lower river tributaries that support vulnerable wild populations (Chilcote 1993, 2003; Hand and Olson 2003; Baker et al. 2008; Chilcote et al. 2011; Ruzycki and Carmichael 2010). All of the challenges described above have made it difficult to estimate stray rates in the Columbia River system, but it has been particularly difficult to disentangle permanent straying from wandering and thermoregulatory behaviors. This distinction is prominent in the Columbia basin because main stem water temperatures are often warmer than those preferred by adult salmon and steelhead migrants. As a result, fish from many summer- and fall-run populations temporarily seek thermal refuge in cooler, non-natal tributaries (*reviewed* in Keefer et al. 2011).

In warm years, a majority of some upriver summer steelhead populations temporarily enter non-natal Columbia River tributaries (High et al. 2006; Keefer et al. 2009) as do significant numbers of fall Chinook salmon (Goneia et al. 2006). Estimating permanent straying into these tributaries using tagged fish is confounded by interception fisheries that harvest thermoregulating migrants (Keefer et al. 2008b, 2009; Clarke et al. 2010, 2011) and by capture at hatchery facilities (Hand and Olson 2003). Additionally, tagged fish used in straying studies are often last detected at

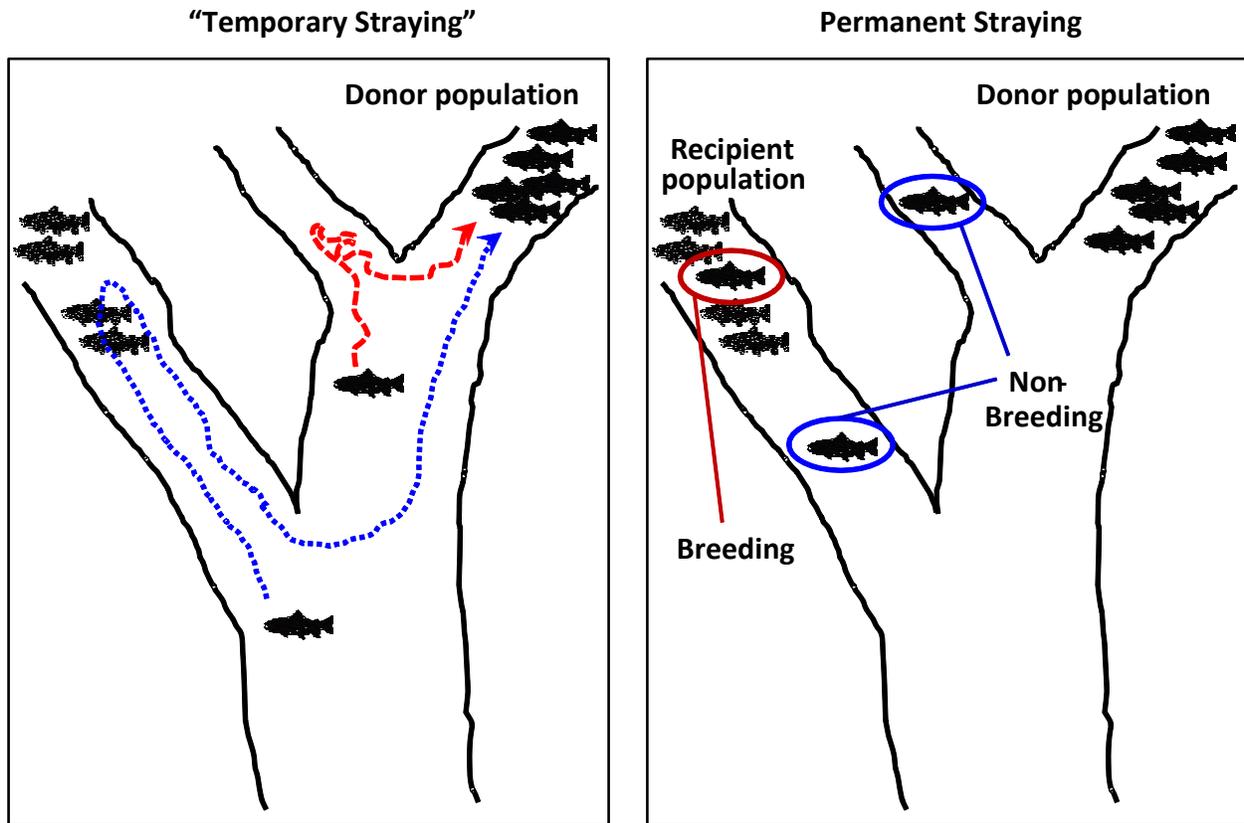


Figure 5. Adult migrants show a variety of ‘temporary’ (left panel) and permanent (right panel) straying behaviors. Temporary straying may be exploratory searching for mates or spawning sites or may be stimulated by environmental conditions such as water temperature. Temporary strays may return to their natal site if they survive their time in the non-natal area. Permanent straying can result in inter-breeding with the recipient population or breeding failure. Permanent strays are a demographic loss from the donor population (shown in color) and may be a demographic gain for the recipient population (shown in grayscale). Straying versus homing status can be ambiguous for fish captured at non-natal hatchery facilities or in fisheries in non-natal sites.

monitoring arrays in the cooler non-natal tributaries but their fate with regards to permanent versus temporary straying is unknown or ambiguous (Ruzycki and Carmichael 2010; Keefer et al. 2011).

A strictly-defined lexicon of straying behaviors that can be applied across species, populations, and geographic regions is almost certainly not feasible. A benchmark at one end of the straying continuum may be breeding at a non-natal location with genetically unrelated conspecifics (i.e., a breeding permanent stray, Figure 5). A second relatively unambiguous category could be permanent strays that breed with other strays, a behavior that is the foundation of range expansion and colonization. Non-breeding permanent strays could be a third group. These fish may fail to find mates or be so phenotypically mismatched with the recipient population (e.g., non-overlapping spawn timing) that breeding is prevented. All three of these categories have strays as a demographic loss from the donor population, but have varying demographic effects on the recipient population. The ambiguous, ‘temporary’ behaviors associated with behavioral thermoregulation, wandering, or exploring of non-natal sites should probably not be associated

with the term ‘straying’. However, these behaviors will continue to be a challenge for straying studies because observation biases and human interventions (i.e., fisheries, hatchery traps, and monitoring methods) result in ambiguous homing outcomes.

4.2 STRAYING MECHANISMS

A variety of inter-related factors potentially determine whether an adult salmon or steelhead strays to a non-natal location. For managers interested in reducing straying (i.e., by hatchery or transported populations), it is important to differentiate outcomes that result from underlying adaptive processes and behaviors from human-influenced factors. In the following sections, we review the mechanisms that can elicit adult straying and attempt to differentiate ‘natural’ biological and ecological processes from factors that are a largely a result of human interventions (i.e., hatchery and transportation effects). Often, the proximate physiological and behavioral mechanisms affecting fish are the same, but the ultimate causal mechanisms differ.

4.2.1 INCOMPLETE JUVENILE IMPRINTING

Although complete imprinting failure is unlikely in either wild or hatchery populations, incomplete imprinting certainly plays a role in adult straying. As described in Section 3.1, imprinting is a dynamic, endocrine-driven process that can occur intermittently across several juvenile life stages. Incomplete imprinting on the natal site may occur when hormone surges are insufficient to stimulate olfactory memories. This may be related to physiological variation among individuals (i.e., in hormone levels or neural development) or to variation in environmental or ecological stimuli (i.e., some fish likely experience fewer stressful events or larger environmental fluctuations). Similarly, species with short freshwater residence times (e.g., chum salmon) may have reduced imprinting opportunity compared to species with extended freshwater residence times like coho and Chinook salmon or steelhead.

Box 6: Straying mechanisms

- **Incomplete imprinting:** a variety of physiological and ecological factors may result in failure to fully imprint on natal sites, rearing sites, or at sequence of sites
- **Interrupted imprinting:** hatchery transfers or juvenile transportation interrupt sequential imprinting
- **Adult sensory impairment:** degeneration of olfactory organs, vision, and other sensory systems can affect navigation and orientation
- **Adult memory failure:** neural degeneration, senescence, and age may impair olfactory memory recall
- **Reproductive behaviors:** avoiding competition, searching for mates, searching for suitable spawning habitat may increase straying
- **Density dependence:** high spawner density may provide attractive homing cues; alternately, competition may stimulate local-scale straying
- **Genetic & life history effects:** some straying behaviors may be hardwired or be a function of life history such as juvenile freshwater residence time, age structure, etc.
- **Attraction to non-natal sites:** environmental, ecological, or landscape-scale cues may attract adults to non-natal sites; attraction may occur with or without rejection of the natal site
- **Hatchery effects:** a variety of hatchery rearing and release practices increase adult straying
- **Displacement / Transportation:** juvenile displacement can dramatically increase adult straying; juvenile transport distance is positively correlated with adult straying

Incomplete imprinting also may occur when juvenile dispersal is unaccompanied by the requisite physiological development. In an example using otolith microchemistry, Hamann and Kennedy (2012) showed that pre-smolt movements away from natal sites led to higher local-scale straying by wild Chinook salmon adults.

Hatchery rearing appears to substantially increase the likelihood of incomplete imprinting. As described in previous sections, hatchery fish have lower hormone and cortisol levels than wild fish (Dittman and Quinn 1996; McCormick et al. 2003) as well as lower olfactory activity and reduced brain development (Marchetti and Nevitt 2003). For these reasons – and probably others – hatchery salmon and steelhead have lower homing success than wild fish across species and populations. More details and specific examples of hatchery effects on adult straying are provided below in Section 5.6.

Environmental toxins have also been shown to negatively affect imprinting. Exposure to some water-borne chemicals such as pesticides, insecticides, heavy metals, and persistent organic pollutants can retard the parr-smolt transformation, reduce olfactory activity, and inhibit neural connectivity (Moore et al. 2007; Arkoosh et al. 2011).

4.2.2 INTERRUPTED JUVENILE IMPRINTING

Interrupted imprinting – in contrast with incomplete imprinting – is primarily associated with human interventions. These include hatchery practices such as inter-basin transfers and outplanting from central rearing facilities. Outplanted and transferred juveniles are often exposed to different olfactory environments in the hatchery versus the outplant location. A temporal component may exacerbate the spatial effects of such transfers, particularly if they occur during periods of olfactory sensitivity or when transfers are mismatched with juvenile smolting.

A second category of interrupted imprinting is the collection and transportation of juveniles that have already initiated migration. Both the behavior (i.e., schooling, negative rheotaxis) and physiology (i.e., PST, elevated hormones) of active migrants prepare them for sequential imprinting along the migration route. However, transportation clearly can interrupt sequential imprinting and the evidence to date suggests that adult straying rates increase with longer juvenile transport distance (Solazzi et al. 1991; Keefer et al. 2008b; Marsh et al. 2012). More details and examples of juvenile transportation effects on adult straying are provided below in Section 5.7.

4.2.3 ADULT SENSORY FAILURE

Straying can also be affected by mechanisms during the adult life stage. Impaired adult navigation or orientation systems that result in fish failure to recognize cues along migration routes clearly reduce homing success. The experiments conducted by Wisby and Hasler (1954) and others using anosmic adult salmon (i.e., with non-functional nasal sacs) showed the primacy of olfaction for homing. Therefore, physiological changes or environmental factors that affect olfactory processes are presumably the most likely to affect adult straying. Impairments to other sensory mechanisms – especially vision (e.g., Ueda 2012) – may play a secondary role.

Salmon maturation and senescence are associated with many changes in the sensory organs, endocrine system, and brains of adult salmonids (see Section 3.6.1). The surge in stress hormones during this life stage may stimulate some olfactory processes and enhance olfactory memory recall (Carruth et al. 2002). However, tissue degeneration, fungal and viral infections, and other declines in physical condition may simultaneously degrade some olfactory and neurological functions (Morbey et al. 2005). Given that the overwhelming majority of adults home rather than stray, the effects of senescence and maturation do not appear to routinely or dramatically impair homing. Nonetheless, the relationships between straying and senescent processes have not been particularly well studied and they may be important for the straying portion of the adult population. For example, mature fish with advanced senescence may select the nearest available spawning location rather than completing migration to the natal site.

As with juveniles, olfactory function and other sensory mechanisms in adult salmon and steelhead are potentially affected by a variety of ambient chemical contaminants (*reviewed by* Klaprat et al. 1992; Tierney et al. 2010). Several studies have demonstrated that exposure to sublethal levels of pesticides (Moore et al. 2001), insecticides (Scholz et al. 2000), and heavy metals (Baldwin et al. 2003, 2011) can reduce olfactory processes and even render fish functionally anosmic. Toxicity studies indicate that these olfactory impairments stem from several mechanisms, including disruptive effects in the central nervous system, reduced or blocked capacity for chemoreception, and olfactory information processing errors (Tierney et al. 2010). Because the olfactory system is continuously linked to the aquatic environment, contaminants can readily come into direct contact with the epithelium and olfactory receptor cells. Therefore, even low toxin concentrations may affect olfactory processing. To date, research on toxin effects on olfaction has been primarily laboratory-based and the degree to which toxins affect salmon and steelhead homing is poorly understood.

4.2.4 ADULT MEMORY FAILURE

Several studies have found associations between adult age and stray rate. Age-related differences have been reported primarily in species with relatively high variation in age at maturity, including Chinook salmon (Quinn and Fresh 1984; Quinn et al. 1991; Unwin and Quinn 1993; Pascual et al. 1995), coho salmon (Labelle 1992), and Atlantic salmon (Jonsson et al. 2003). In most of these studies, older salmon strayed at higher rates than those in younger age classes. The Jonsson et al. (2003), Unwin and Quinn (1993), and Pascual et al. (1995) studies showed a relatively large age effect, with older adults straying at substantially higher rates than younger fish in both wild and hatchery populations. These age results were confounded somewhat by juvenile age and release timing, indicating that some age-related straying was a result of carryover effects from juvenile experiences.

Notably, other studies have found no age effect on straying in Chinook salmon. Candy and Beacham (2000) and Hard and Heard (1999) reported higher straying by younger adults. The latter study found that younger Chinook salmon (measured by years at sea) strayed at higher rates than older fish. Higher straying by younger salmon was driven, in part, by the higher relative abundance of males in the younger age classes (including jacks) and higher straying by males versus females.

A general hypothesis for age-mediated straying has been that older fish spend more time in the ocean away from their natal river system and hence are less able to either recognize (or perhaps remember) their natal site odor. A related hypothesis is that subtle changes in the olfactory bouquet produced by the natal site are more likely to develop over longer time periods. Neither of these hypotheses have much direct empirical support, although there is some indirect evidence (i.e., studies showing decline in memory recall in older organisms). Unfortunately, the most compelling data demonstrating higher straying by older fish has been derived from hatchery populations. Hatchery practices, including juvenile size and age at release and release timing effects, interact in complex ways with adult return rates and adult homing behaviors, often making interpretation difficult.

4.2.5 REPRODUCTIVE BEHAVIOR / DENSITY DEPENDENCE

In some cases, local-scale straying may be driven more by reproductive behaviors than by any sensory impairment or homing ‘failure’ per se. As described in Section 3.6.3, searching for mates or suitable spawning habitat can result in movements away from natal sites. Such behaviors appear to be more likely for males than females, on average, and may be more common in systems where spawning habitats are relatively unstable through time. It is not clear, however, to what degree exploratory movements associated with reproduction occur at sites distant (e.g., 10’s-100’s of kilometers) from natal spawning areas.

Intra-specific and density-dependent effects can influence exploratory movements and testing behaviors. For example, there is some evidence that homing success is higher in years with abundant adult returns, perhaps because social or chemical cues increase with abundance (Sholes and Hallock 1979; Quinn and Fresh 1984). Alternately, local-scale straying can increase when natal spawning habitats are saturated (Mortensen et al. 2002; Lin et al. 2011), because moving to nearby non-natal sites allows adults to locate uncontested redd sites (females) and uncontested mates (males). Lin et al. (2011), for example, described how strays from large source populations of chum and Chinook salmon routinely formed small breeding aggregations in nearby Alaskan rivers.

Low spawner density at the natal site also may affect straying rates. Such conditions arise when the natal population is very small or when adverse environmental conditions deter fish from the natal area (e.g., Leider 1989; Thorpe 1994).

4.2.6 GENETIC & LIFE HISTORY EFFECTS

The role of genetics in adult straying remains an open question. Certainly a variety of innate exploring and searching behaviors contribute to straying, but the specific stimuli that result in the up-regulation of genes that affect permanent straying are unknown. Some of the variation in homing and straying among species (Figure 6) presumably evolved in response to locally-adaptive selective pressures (Hendry et al. 2004; Quinn 2005). For example, populations that evolved in temporally stable habitats (e.g., sockeye or Chinook salmon spawning in low-gradient, high-elevation streams) are less prone to straying than populations that evolved in

dynamic habitats (e.g., chum salmon spawning in intertidal river deltas or winter steelhead in flood-prone coastal watersheds).

Life history characteristics appear to be predictive of straying differences among species and populations, especially variability in juvenile freshwater residence time and behavior (i.e., moving among habitats) and adult age structures (Figure 6). Thorpe (1994) suggested that complex multiple-age structures like those of Chinook salmon and steelhead are more likely to be associated with precise homing because the risk of reproductive failure is distributed across years. Thus, risks from adverse or catastrophic environmental conditions at the natal site in any given year are spread across cohorts. In contrast, simple age structuring like that of pink and chum salmon has been associated with less precise homing and higher straying because adults must find alternate habitats when conditions are poor at natal sites (Quinn 1993; Thorpe 1994). Life history characteristics can produce phenotypically divergent adults (e.g., in migration timing, spawn timing, or morphological traits), and each of these factors also may contribute to differential straying rates (e.g., Lin et al. 2008).

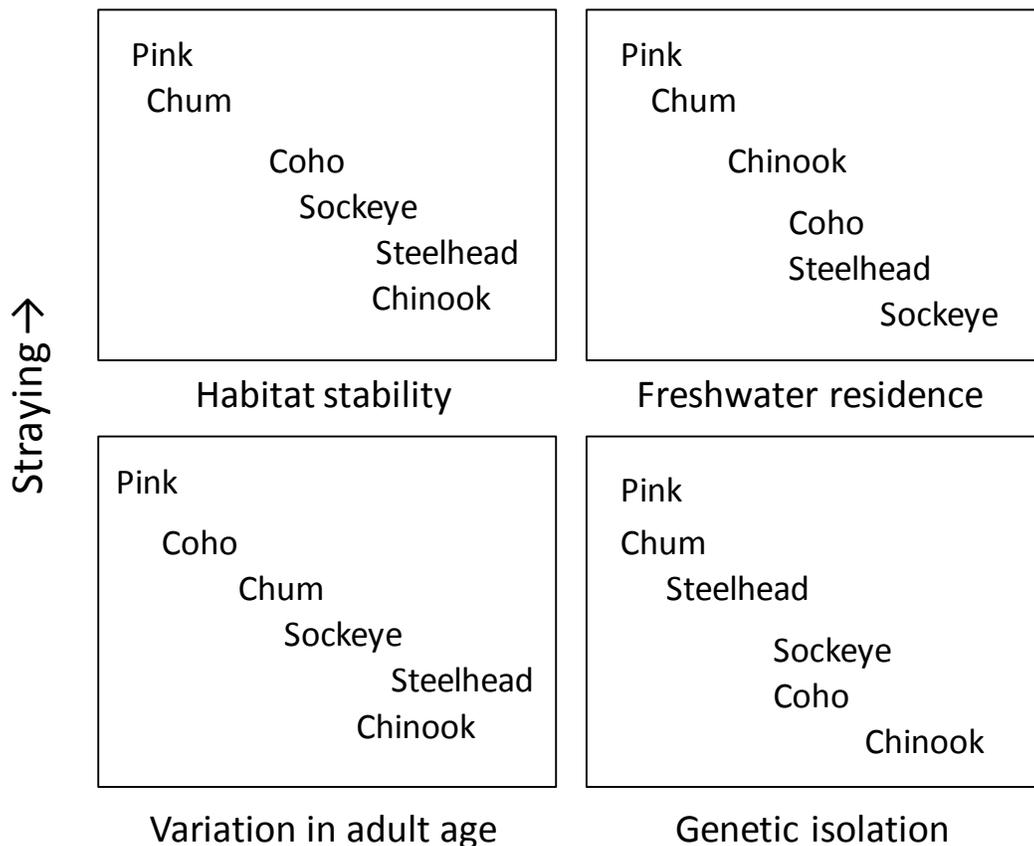


Figure 6. Hypothetical relationships between adult straying by Pacific salmon and steelhead species and habitat stability, juvenile freshwater residence time (or complexity), variation in adult age, and genetic isolation (a measure of gene transfer and dispersal among populations). Figure was modified from a presentation by T. Quinn to US Army Corps of Engineers, April 2011.

4.2.7 ATTRACTIVENESS OF NON-NATAL SITES

The reason(s) that straying adults select one non-natal site over other available locations is not well understood, yet some recipient systems are clearly favored. Spatial proximity to the natal site is certainly one of the most important predictors. Many straying studies have reported exponential declines in the number of strays with increasing distance from the home site (Unwin and Quinn 1993; Quinn and Fresh 1984; Candy and Beacham 2000; Thedinga et al. 2000; Bartron et al. 2004; Correa and Gross 2008). Several of these case studies reported that substantial majorities of recovered strays entered rivers within 10-50 km of the natal river mouth. Notably, some nearby rivers were only slightly used or were ignored altogether by strays, suggesting that other ecological or environmental factors affected site selection. The effect of spatial distance appears to be compounded in some large and complex river systems. For example, gene flow among chum salmon was much higher in a group of short coastal rivers – where among-site straying rates were high – than in the large Yukon River system where straying was apparently infrequent (Olsen et al. 2008). The authors attribute the difference to greater local adaptations to the diverse Yukon River habitats. Indeed, this spatial, isolation-by-distance organization is fundamental to the metapopulation structure of salmonids (Hendry et al. 2000, 2004; Waples et al. 2004, 2008; Olsen et al. 2010).

Physical and chemical properties of recipient systems also may attract strays. These potentially include water temperature, river discharge, oxygen levels, and olfactory signatures. Adjacent rivers and streams often have very similar physiochemical characteristics, especially when drainages are small (i.e., adjacent creeks), and this surely affects the spatial distribution of strays described above. A recent Chinook salmon study by Dittman et al. (2010) and Cram et al. (2012) showed how relatively local scale differences in spawning habitat quality affect the distribution of adults, with higher local straying when conditions at the home site are less favorable. Similar processes may occur at larger scales because rivers with longer geographic distances between their outlets can also share attractive qualities. For example, distant river mouths may have watersheds that have similar climate, geology, and terrestrial inputs that result in similar physiochemical signatures. This appears to occur in the rivers draining the Columbia River plateau (e.g., Deschutes, John Day, Umatilla, Walla Walla, Tucannon, Grande Ronde) where relatively high among-basin stray rates have been reported for spring and fall Chinook salmon and summer steelhead.

5.0 SYNTHESIS OF STRAYING DATA

5.1 DATA CHALLENGES

Although there is a relatively large literature describing adult salmon and steelhead straying, we found it difficult to directly compare results across studies. Most of the peer-reviewed research of stray rates either *from* or *into* a population has reported on hatchery fish and most of these studies have had site-specific or experimental elements that confound direct comparisons across studies. Most often, this included some group of fish that were either transferred or outplanted to a site other than the rearing site or included fish that were reared at a location other than their ancestral site. Furthermore, one or more of the straying estimation challenges described in Section 4.1 occurred in most studies.

We selected 62 studies to provide a general summary of the types of straying data that have been collected in the Columbia River basin (Table 1) and at sites outside the basin (Table 2). These studies are a reasonably representative subsample, though we made an effort to include both a range of study types (e.g., tagging studies, genetic studies, carcass surveys, etc.) and to include a variety of species. We also included most of the Columbia River transportation studies, as these were most directly relevant to the review objectives for the USACE. Some agency projects in the Columbia River basin have not been peer-reviewed, but we have included them given their direct relevance.

Broad-scale patterns certainly emerged regarding differences among species and life history types, among hatchery or ranched fish versus wild fish, and in relation to transplantation and transportation effects. However, we caution against over-interpretation of any individual stray rate estimates in the summaries presented below.

5.2 GENERAL PATTERNS

Most straying estimates in the Columbia River basin and elsewhere have relied on tagged fish, and especially on fish with coded wire tags (Tables 1 and 2). A variety of other marks have also been used (fin clips, otolith marks, etc.) and there has been a recent shift to using genetic techniques to infer stray rates.

Even with the considerable uncertainty that accompanies the different methods used to estimate straying, there appear to be some inherent differences in stray rates among species (Box 7). Multi-species reviews by Hendry et al. (2004),

Box 7: Mean donor population straying (%)

* These estimates are gross generalizations. A mix of study methods and populations were combined and some species had far fewer estimates and geographical representation than others.

	<u>Pess (2009)</u>	<u>This review</u>
● Chum salmon	19.1	28.4
● Pink salmon	15.4	8.4
● Sockeye salmon	0.8	2.4
● Coho salmon	7.8	9.8
● Spring Chinook salmon	6.2	3.4
● Fall Chinook salmon	--	34.9
● Steelhead	7.7	13.8
● Atlantic salmon	7.7	10.1

Table 1. Representative straying studies from the Columbia River basin. Study # is for referencing the data presented in Figures 7-9.

Study #	Reference	Year	Species	Location	Primary Method(s)	Transfer / Outplant	Barge/Truck Transport
1	Quinn & Fresh	1984	Chinook	Cowlitz River	CWT		
2	Leider	1989	Steelhead	Lower Columbia tributaries	n/a		
3	Quinn et al.	1991	Fall Chinook	Lower Columbia tributaries	CWT		
4	Keefer et al.	2005	Multiple	Upper Columbia, Snake, Yakima	RT		
5	Milks et al.	2006	Fall Chinook	Lyons Ferry H., Tucannon River	Carcass		
6	Arnsberg et al.	2007	Fall Chinook	Clearwater River	Carcass, CWT		
7	Narum et al.	2008	Chinook	John Day River	Genetic		
8	Ruzycki & Carmichael	2010	Steelhead	John Day River	Carcass,PIT		
9	Gallinat & Ross	2011	Chinook	Tucannon River	PIT, CWT		
10	Bumgarner & Dedloff	2011	Steelhead	Tucannon River	PIT		
11	Hamann & Kennedy	2012	Chinook	MF Salmon River	Otolith		
12	Matala et al.	2012	Chinook	SF Salmon River	Genetic		
13	Pascual et al.	1995	Fall Chinook	Grays & Washougal rivers	CWT	Yes	
14	McIsaac & Quinn	1988	Fall Chinook	Columbia River hatcheries	CWT	Yes	
15	Hayes & Carmichael	2002	Fall Chinook	Umatilla & Snake rivers	CWT	Yes	
16	Garcia et al.	2004	Fall Chinook	Clearwater & Snake rivers	RT	Yes	
17	Schroeder et al.	2007	Chinook	Willamette River	CWT	Yes	
18	Murdoch et al.	2009	Sockeye	Wenatchee River	RT	Yes	
19	Clarke et al.	2010	Steelhead	Grande Ronde & Imnaha rivers	CWT	Yes	
20	Dittman et al.	2010	Chinook	Yakima River	CWT, Eye tags	Yes	
21	Clarke et al.	2011	Steelhead	Grande Ronde River	CWT	Yes	
22	Ebel et al.	1973	Chinook, Steelhead	Snake River	CWT, Brand		Yes
23	Slatick et al.	1975	Chinook, Steelhead	Snake River	CWT, Brand		Yes
24	Vreeland et al.	1975	Coho	Little White Salmon Hatchery	Fin clips		Yes
25	Ebel	1980	Chinook, Steelhead	Snake River	CWT, Brand		Yes
26	McCabe et al.	1983	Coho	Willard Hatchery	CWT		Yes
27	Bjornn & Ringe	1984	Chinook, Steelhead	Snake	CWT		Yes
28	Solazzi et al.	1991	Coho	Cascade Hatchery	CWT, Fin clips		Yes
29	Bugert et al.	1997	Fall Chinook	Snake River, Lyons Ferry H.	CWT		Yes
30	Chapman et al.	1997	Chinook, Sockeye	Upper Columbia River	CWT, Brand, Jaw		Yes
31	Keefer et al.	2008b	Chinook, Steelhead	Snake River	PIT, RT		Yes
32	Marsh et al.	2012	Chinook, Steelhead	Snake River	PIT		Yes

Table 2. Representative straying studies from sites outside the Columbia River basin. Study # is for referencing the data presented in Figures 7-9.

Study #	Reference	Year	Species	Location	Primary Method	Transfer / Outplant	Barge/Truck Transport
33	Shapovalov & Taft	1954	Coho, Steelhead	California	Fin clips		
34	Labelle	1992	Coho	British Columbia	CWT		
35	Unwin & Quinn	1993	Chinook	New Zealand	CWT		
36	Sharp et al.	1994	Pink	Alaska	CWT		
37	Tallman & Healey	1994	Chum	British Columbia	Fin clips		
38	Griffith et al.	1999	Sockeye	Washington	T-bar tag		
39	Wertheimer et al.	2000	Pink	Alaska	CWT		
40	Insulander & Ragnarsson	2001	Atlantic	Sweden	Carlin		
41	Mortensen et al.	2002	Pink	Alaska	CWT		
42	Jonsson et al.	2003	Atlantic	Norway	Carlin		
43	Bartron et al.	2004	Steelhead	Michigan	Genetic		
44	Gilk et al.	2004	Pink	Alaska	Genetic		
45	Vasemägi et al.	2005	Atlantic	Sweden	Genetic		
46	Lin et al.	2008	Sockeye	Alaska	Genetic		
47	Brenner et al.	2012	Pink, Chum, Sockeye	Alaska	Otolith		
48	Wagner	1969	Steelhead	Oregon	Fin clips	Yes	
49	Gunnerød et al.	1988	Atlantic	Norway	Carlin	Yes	
50	Lirette & Hooton	1988	Steelhead	British Columbia	CWT	Yes	
51	Quinn et al.	1989a	Coho	Washington	CWT	Yes	
52	Johnson et al.	1990	Coho	Oregon	CWT	Yes	
53	Hansen & Jonsson	1991	Atlantic	Norway	Tags	Yes	
54	Slaney et al.	1993	Steelhead	British Columbia	CWT	Yes	
55	Hansen & Jonsson	1994	Atlantic	Norway	Carlin	Yes	
56	Isaksson et al.	1997	Atlantic	Iceland	CWT	Yes	
57	Dempson et al.	1999	Atlantic	Newfoundland	RT, Floy	Yes	
58	Hard & Heard	1999	Chinook	Alaska	CWT	Yes	
59	Candy & Beacham	2000	Chinook	British Columbia	CWT	Yes	
60	Kenaston et al.	2001	Steelhead	Oregon	Fin clips	Yes	
61	Schroeder et al.	2001	Steelhead	Oregon	Fin clips	Yes	
62	Gorsky et al.	2009	Atlantic	Maine	PIT	Yes	

Quinn (2005), and Pess (2009) generally align with the estimates we derived from the data in Figures 7 and 8. In relative terms, species with shorter juvenile freshwater residency and shorter freshwater migration distances (e.g., chum, pink, and some ocean-type Chinook salmon) had higher reported donor straying rates than other species. The lowest mean estimates were for stream-type Chinook salmon and sockeye salmon. Coho salmon, Atlantic salmon, and steelhead had intermediate mean values (Box 7).

Studies that directly compared straying between species or between life history types within a shared river system and migration year were very uncommon. A few exceptions included the study of winter steelhead and coho salmon by Shapovalov and Taft (1954) and several of the transportation and radiotelemetry studies in the Columbia-Snake (e.g., Ebel 1980; Bjornn and Ringe 1984; Chapman et al. 1997; Keefer et al. 2005, 2008b; Marsh et al. 2012). The latter group, however, typically included an aggregation of contributing populations, resulting in reduced inferential opportunity.

5.3 DONOR POPULATION STRAY RATES: COLUMBIA RIVER BASIN

5.3.1 FALL CHINOOK SALMON

Several Columbia River studies have estimated adult stray rates for ocean-type (i.e., subyearling emigration) Chinook salmon (Table 1, Figure 7). These studies were reasonably well distributed across the basin, and included hatchery populations from the lower river (e.g., McIsaac and Quinn 1988; Pascual et al. 1995; Quinn et al. 1991), the Umatilla River (e.g., Hayes and Carmichael 2002), and several lower Snake and Clearwater River hatchery groups (e.g., Bugert et al. 1997; Garcia et al. 2004; Keefer et al. 2005; Milks et al. 2006; Arnsberg et al. 2007). The Keefer et al. (2005) study also included a relatively large sample of summer or summer–fall Chinook salmon from the upper Columbia River that included fish with an ocean-type life history.

Reported stray rates for fall and summer–fall Chinook salmon were higher and more variable than for other Columbia River species (Figure 7). Median rates ranged from about 1% in the control groups in the McIsaac and Quinn (1988) study, to ~10% in the coded wire tag study of Lyons Ferry Hatchery fish by Bugert et al. (1997) and the radiotelemetry study by Keefer et al. (2005), to more than 50% by experimental groups released in the Umatilla River (Hayes and Carmichael 2002). Many salmon in the latter study passed (i.e., overshot) the Umatilla River and strayed into the lower Snake River. There was a similar overshoot tendency in Lyons Ferry Hatchery studies, where fall Chinook salmon passed the hatchery and continued up the Snake River (e.g., Milks et al. 2006).

Fall Chinook salmon in the lower Columbia River studies by Pascual and Quinn (1994) and Pascual et al. (1995) had relatively large sample sizes and provided some of the earliest systematically collected straying data in the Columbia basin. These studies indicated relatively high rates of regional straying (many estimates were >30%), with most strays collected in other lower Columbia River tributaries and hatcheries.

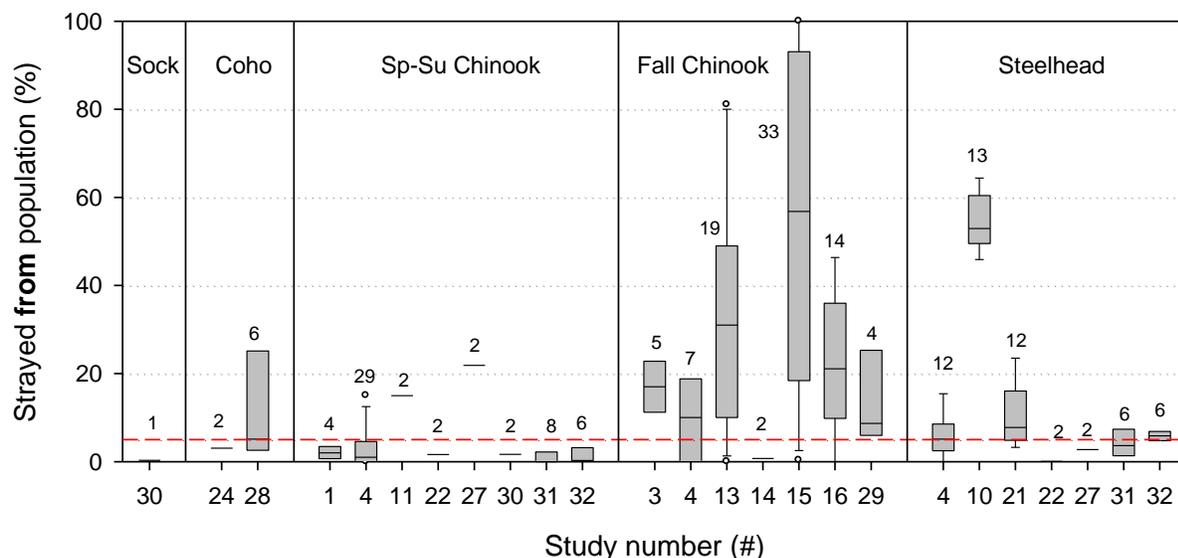


Figure 7. Estimates of adult salmon and steelhead stray rates from donor populations in the Columbia River basin. Study numbers (X-axis) refer to the studies in Table 1. Numbers above boxes represent the number of independent point estimates of straying in each study. Boxes show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Horizontal red line is at 5%. Methods differed widely across studies and values represent minimum stray rates because not all potential recipient populations were monitored in most studies.

Garcia et al. (2004) showed that radio-tagged adult fall Chinook salmon strayed at relatively high rates (*median* ~ 20%) among spawning areas in the Clearwater River and Snake River above Lower Granite dam. These fish were reared and acclimated at several locations, and the authors suggested that juvenile imprinting on rearing sites contributed to adult straying. About 4% of the radio-tagged fall Chinook salmon in Keefer et al. (2005) strayed, with rates ranging from $\leq 1\%$ for Lyons Ferry Hatchery fish released on site to $> 15\%$ for salmon from the Yakima and Umatilla rivers and for those barged downstream from Snake River dams.

Summer–fall Chinook salmon from Wells Hatchery released at various locations in the upper Columbia basin strayed at rates of 5-8% (Keefer et al. 2005). In the same study, salmon reared at East Bank Hatchery and those collected and tagged as juveniles at Rocky Reach and Rock Island dams strayed at rates of 0-1%. Differences in juvenile rearing and outplanting procedures likely contributed to variability among groups.

5.3.2 SPRING CHINOOK SALMON

Estimates of donor population straying by Columbia River spring Chinook salmon have consistently been $< 5\%$, though some case studies have had estimates ranging to more than 20% (Figure 8). The higher estimates have generally been associated with small sample sizes, such as the Bjornn and Ringe (1984) transport study or the Umatilla River sample in Keefer et al. (2005), or were affected by the spatial scale used to define straying. For example, relatively high local-scale straying was estimated by Hamann and Kennedy (2012) in the Middle Fork Salmon River, whereas most other spring Chinook studies only examined straying at larger spatial scales. The

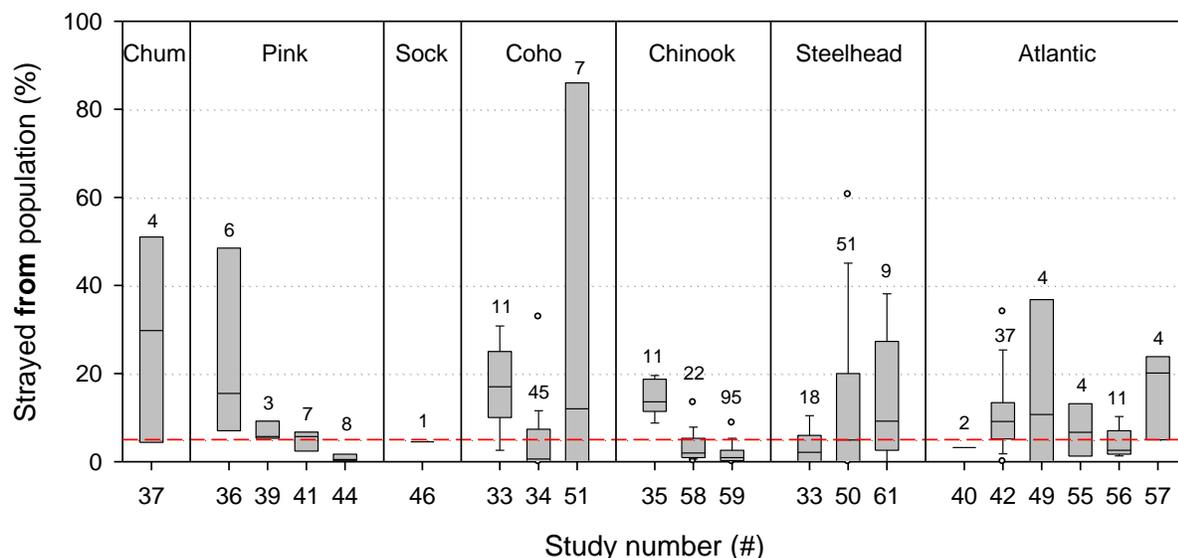


Figure 8. Estimates of adult salmon and steelhead stray rates from donor populations outside the Columbia River basin. Study numbers (X-axis) refer to the studies in Table 2. Numbers above boxes represent the number of independent point estimates of straying in each study. Boxes show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Horizontal red line is at 5%. Methods differed widely across studies and values represent minimum stray rates because not all potential recipient populations were monitored in most studies.

spring Chinook homing study by Dittman et al. (2010) was another relatively local-scale evaluation, and spawner distributions were complicated by a variety of rearing, acclimation, and release strategies. We did not include estimates from this study in Figure 8 given the ambiguity in what constituted straying.

The geographic and temporal representation of spring Chinook straying studies has been somewhat limited in the Columbia basin. There are donor population case studies from the Cowlitz River (Quinn and Fresh 1984), from sub-basins of the Salmon River (Hamann and Kennedy 2012; Matala et al. 2012), from the Snake River transportation program (Ebel 1980; Keefer et al. 2008b; Marsh et al. 2012), from the upper Columbia transportation program (Chapman et al. 1997), and from the Willamette River (Schroeder et al. 2007). The radiotelemetry evaluation by Keefer et al. (2005) included several small to modest-sized samples from the Wind, John Day, Yakima, Icicle, Clearwater, Grande Ronde, Salmon and Imnaha rivers.

Spring Chinook salmon in the above studies tended to stray into nearby rivers, particularly in the absence of interventions like juvenile transport or hatchery outplanting. As examples, Cowlitz River salmon mostly entered other lower Columbia River tributaries (Quinn and Fresh 1984), Wind River salmon mostly entered other Bonneville reservoir tributaries (Keefer et al. 2005), and South Fork Salmon River fish mostly strayed into non-natal tributaries within the South Fork drainage (Matala et al. 2012). Among-basin straying in the Willamette River basin has largely been associated with hatchery fish and a variety of outplanting and supplementation programs (Schroeder et al. 2007; also see review by Keefer and Caudill 2010).

In contrast, spring (and summer) Chinook salmon from the upper Columbia River and those transported in the Snake River have mostly been recorded straying into lower and mid-Columbia River tributaries like the Little White Salmon, Wind, Deschutes, and John Day rivers (Bjornn and Ringe 1985; Chapman et al. 1997; Keefer et al. 2005, 2008b; Marsh et al. 2012). Notably, these studies generally did not estimate straying to tributaries upstream of transportation collection sites. Stray identification challenges associated with hatchery trapping and fishery harvest were common in the spring Chinook research.

5.3.3 COHO SALMON

There has been little straying research on Columbia River coho salmon. The study by Vreeland et al. (1975) used hatchery coho reared at Little White Salmon Hatchery and released either on site or in Youngs Bay outside the Columbia River. Strays from the on-site hatchery release group were recovered in four other lower Columbia River hatcheries resulting in point estimates of 1.0% and 6.8% in the two study years.

Two other Columbia River coho salmon studies included transportation. McCabe et al. (1983) reported higher (though not quantified) straying by coho salmon that were transported in trucks from Klickitat Hatchery compared to an on-site control group. The experimental transport study by Solazzi et al. (1991) found that coho salmon that were trucked as juveniles from a hatchery near Bonneville Dam increasingly strayed as the transport distance increased. Whereas < 0.1% of the on-site control group was recorded straying to sites outside the Columbia River basin, estimates were 3.4%, 4.1%, 6.1%, 21.0%, and 37.5% for groups that were transported approximately 205, 232, 253, 253, and 272 kilometers, respectively. The latter three groups were transported to either the Columbia River plume or to sites 19 and 38 km offshore from the Columbia River mouth.

5.3.4 SOCKEYE SALMON

There has been little straying research on Columbia or Snake River sockeye salmon. Anecdotal reports from radiotelemetry studies by Naughton et al. (2005) and Keefer et al. (2008e) indicate that there may be some sockeye salmon straying into tributaries along the migration corridor. Strays in these studies were reported in lower Columbia River tributaries (1.7% of fish tagged at Bonneville Dam) and into the Clearwater River (3.2% of a small sample tagged at Lower Granite Dam). These authors suggested that some of the sockeye salmon straying may have been related to behavioral thermoregulation and possibly harvest. In a transportation study, Chapman et al. (1997) found that upper Columbia River sockeye salmon strayed into lower Columbia River tributaries at low rates, but noted that the sampling effort to identify strays was limited.

Murdoch et al. (2009) investigated local-scale sockeye salmon straying for a population released as parr from net pens in Lake Wenatchee. They concluded that net-pen fish were less able to imprint on a natal stream and consequently the distribution of adults among Wenatchee spawning areas differed between net-pen and naturally reared fish, with net-pen fish reported at sites more distant from spawning sites used by natives.

5.3.5 STEELHEAD

Most estimates of steelhead straying in the Columbia River basin have been for Snake River summer-run populations. We found few peer-reviewed estimates of straying by winter run fish, although there has been some research on summer-run fish that stray into winter-run populations in the Willamette River basin (Chilcote 2003; Kostow et al. 2003; Kostow and Zhou 2006) and Leider (1989) described winter steelhead straying following the eruption of Mount St. Helens. Median donor population straying estimates in the reviewed research were typically between 3% and 10%, although some point estimates were considerably higher (Figure 8). The highest estimates in Figure 8 (*mean* = 55%) were for Tucannon River steelhead that overshot the Tucannon and were last recorded in the Snake River at or upstream from Lower Granite Dam (Bumgarner and Dedloff 2011). Similar overshoot patterns were reported for radio-tagged steelhead from Lyons Ferry Hatchery, and some of these strays were recovered in small tributaries to Lower Granite reservoir and to Dworshak Hatchery in the Clearwater River basin (Mendel and Schuck 1989).

The migratory behaviors and life history of steelhead lead to more ambiguous homing / straying outcomes than for other Columbia River species. In particular, the tendency for thermoregulatory behavior along the migration route leads to considerable steelhead harvest in non-natal tributary fisheries. For example, the straying estimates presented for Grande Ronde River steelhead (*mean* = 11%, *range* = 4-25%) by Clarke et al. (2011) included many steelhead that were reported harvested in the Deschutes River. Marsh et al. (2012) estimated that 4-9% of PIT-tagged Snake River steelhead strayed into the Deschutes or John Day rivers and Ruzycki and Carmichael (2010) estimated that 1.7-3.5% of barged Snake River steelhead strayed into the John Day River in 2007-2009; each of these estimates did not attempt to control for harvest. For comparison, Keefer et al. (2008b) excluded Snake River steelhead that were reported harvested in non-natal tributaries and then estimated stray rates into lower Columbia River tributaries of 2-7% for non-transported fish and 7-9% for transported fish. The latter study included several more straying locations than either Clarke et al. (2011) or Marsh et al. (2012).

There appear to be large differences in steelhead stray rates among donor hatchery populations. Carmichael and Hoffnagle (2006), for example, showed that some Snake River hatcheries produce far more strays than others. In particular, steelhead from Wallowa and Pahsimeroi hatcheries were far more likely to stray into the Deschutes River than were steelhead from Dworshak Hatchery. These differences may have been related to the migration timing of adults (much later, on average, for Dworshak steelhead), or to differences in rearing and release procedures (e.g., transfer among hatcheries, pre-release, acclimation, etc.).

5.4 DONOR POPULATION STRAY RATES: NON-COLUMBIA SITES

Straying estimates derived from donor populations outside of the Columbia River basin were broadly similar to those from the Columbia River basin, with relatively high variability among species and among study populations (Figure 9). Mean estimates for spring Chinook salmon were < 5% in Hard and Heard (1999) and Candy and Beacham (2000), which were two well-designed and data-rich straying studies. The relatively higher (*mean* = 14%) spring Chinook straying reported by Unwin and Quinn (1993), may have been because the New Zealand study

population was introduced and/or because there were a variety of rearing and release methods. The mean estimates for steelhead were ~4% (Shapovalov and Taft 1954), ~13% (Lirette and Hooton 1988), and 14% (Schroeder et al. 2001). These estimates may have averaged higher than those in the Columbia River basin, at least in part, because many of the study populations were hatchery fish and many were winter-run steelhead from coastal watersheds. Estimates for coho salmon were quite variable. We considered the study by Labelle (1992) to be the most ‘realistic’ representative of coho straying (*mean* = 5%) because it included multiple hatchery and wild populations monitored over several years. As in the Columbia basin, we did not find many estimates of sockeye salmon straying, although the published data do suggest relatively low stray rates, at least at intermediate to large spatial scales.

Straying estimates for species not studied in the Columbia River basin (chum, pink, and Atlantic salmon) varied among populations in ways that were similar to the Columbia River species. Most of these studies relied on hatchery or farm-raised salmon, and included a variety of management-related experimental approaches.

5.5 RECIPIENT POPULATION STRAY RATES

Straying estimates into recipient populations are relatively uncommon relative to donor population estimates. However, there have been several recent recipient-based studies in river systems with relatively high proportions of strays versus natives (Figure 9). The multi-species study by Brenner et al. (2012), which included surveys at many recipient sites, recorded widely varying percentages (i.e., 0% to near 100%) of hatchery chum, pink, and sockeye salmon strays in the rivers and streams draining into Prince William Sound. Schroeder et al. (2001) estimated that hatchery winter steelhead strays made up 4-43% of populations in coastal Oregon rivers. Similarly, the Atlantic salmon study by Isaksson et al. (1997) reported stray rates averaging near 20% for recipient populations; this study included large numbers of pen-raised fish. Estimates have been considerably lower for wild Atlantic salmon. The coho salmon study by Labelle (1992) also found consistently low stray rates into recipient populations on Vancouver Island.

In the lower Columbia River basin, Schroeder et al. (2007) reported a wide range of recipient-based stray estimates for Willamette River basin spring Chinook salmon. On average, ~23% of the sampled fish were strays in various sub-basins and most were derived from Willamette hatchery populations. In the mid-Columbia, recipient-based straying was estimated in the Deschutes River by Hand and Olson (2003) and Carmichael and Hoffnagle (2006) and in the John Day River by Narum et al. (2008) and Ruzycski and Carmichael (2010). These studies all focused on straying by Snake River hatchery steelhead. The Hand and Olson (2003) report showed that hatchery strays have accounted for > 50% of the total steelhead returns to Warm Spring River, a major Deschutes River tributary. They also showed that annual counts at Sherars Falls on the main Deschutes included stray numbers that ranged from several hundred in the early 1980s to more than 10,000 in each year between 1995 and 2003. Origin hatcheries for these strays – when they were identifiable – included Irrigon-Grande Ronde, Wallowa, and Imnaha.

Carmichael and Hoffnagle (2006) used some of the same data sources at Hand and Olson (2003), but also reported annual percentages of strays to the Deschutes River above Sherars Falls. From

1977-2003, their recipient population stray estimates above the falls ranged from <10% to >70%, with the highest percentages in the mid-1990s. This study indicated that strays from various Snake River steelhead hatcheries had different spatial and temporal distributions within the

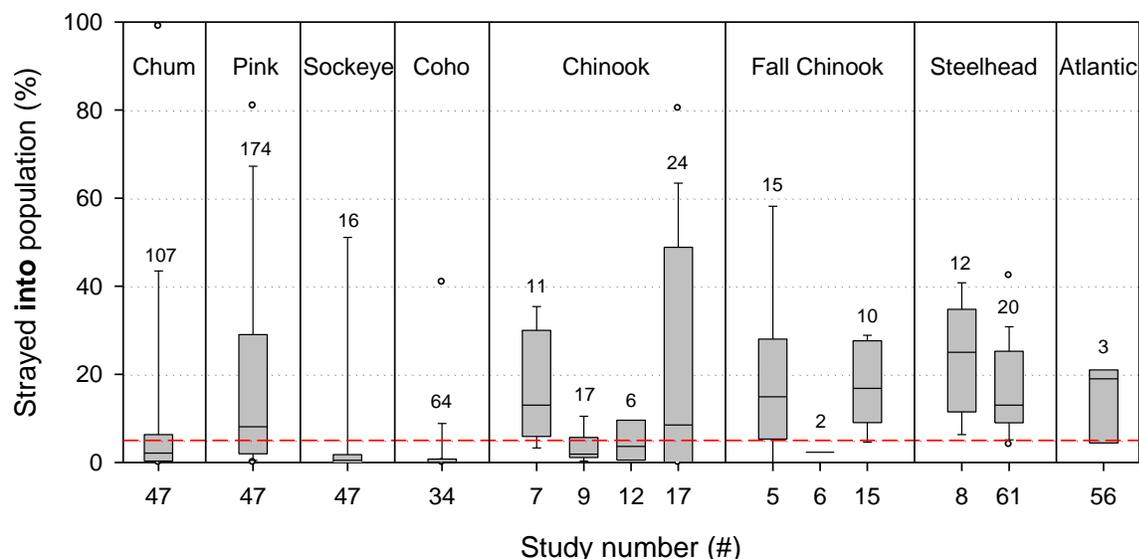


Figure 9. Estimates of adult salmon and steelhead stray rates into recipient populations both within and outside of the Columbia River basin. Study numbers (X-axis) refer to the studies in Tables 1 and 2. Numbers above boxes represent the number of independent point estimates of straying in each study. Boxes show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Horizontal red line is at 5%. Methods differed widely across studies and values represent minimum stray rates because not all potential recipient populations were monitored in most studies.

Deschutes River. Hatchery practices, life history differences such as adult migration timing, and other factors presumably affected differences in straying behaviors among hatchery groups. In both Hand and Olson (2003) and Carmichael and Hoffnagle (2006), a variety of methods were used to estimate straying, including counts, hatchery and trap recoveries, surveys in spawning areas, and harvest data. Unknown proportions of the non-harvested strays eventually exited the Deschutes River. Hence, concrete estimates of permanent, breeding steelhead strays were not possible.

In the John Day River, Ruzycski and Carmichael (2010) reported that thousands of hatchery steelhead strays have been observed in spawner surveys. On average, 23% of adult steelhead captured in seines and screw traps in the John Day River and ~7-41% of observed spawners were hatchery strays. Detections of PIT-tagged steelhead in the lower John Day River, and coded wire tag data, suggest that the majority of steelhead straying into the basin originated in the Snake River.

Narum et al. (2008) used genetic assignments to identify spring Chinook salmon strays at four John Day River spawning sites in 2004-2006. They estimated that Snake River Chinook salmon made up 3-36% (*mean* =16%) of the samples. Many additional salmon could not be assigned to origin, indicating that strays likely made up a larger portion of the escapement to these sites than the estimates that were reported.

In the Snake River basin, recipient population stray estimates have been made for spring and fall Chinook salmon in the Tucannon River (Milks et al. 2006; Gallinat and Ross 2011). On average, ~20% of the fall Chinook salmon escapement ($n = 15$ years) and ~4% of the spring Chinook escapement ($n = 17$ years) into the Tucannon River were strays. Sources for the spring and/or fall Chinook salmon strays into the Tucannon River included the Umatilla River, Lyons Ferry Hatchery, and various other Snake River and Columbia River basin donor groups. Further upstream, Blankenship and Mendel (1993, 1997) reported that 4-26% of adult fall Chinook salmon and 10-35% of jack fall Chinook salmon at Lower Granite Dam originated from hatcheries outside of the Snake River, and especially from the Umatilla River. In the South Fork Salmon River, Matala et al. (2012) cited tribal data for hatchery spring Chinook straying into Johnson Creek and the Secesh River, with mean estimates of ~3-4%.

A series of studies estimated straying by hatchery steelhead into Alpowa Creek – a tributary to the Lower Granite reservoir – and Asotin Creek – a Snake River tributary above Lower Granite Dam (Mayer et al. 2010; Crawford et al. 2012). Annual estimates of hatchery strays captured at the Asotin Creek weir averaged 11% (*range* = 5-18%) from 2005-2011. The percentage of strays was higher in Alpowa Creek, averaging 46% (*range* = 23-65%; 2008-2011). Source hatcheries were generally unknown, although some fish originated from Lyon's Ferry Hatchery and the Tucannon River. Hatchery strays were documented at similar rates at other small tributaries near Asotin Creek.

5.6 HATCHERY AND OUTPLANTING EFFECTS

A recurrent data pattern in the reviewed straying studies was that juveniles that were either outplanted or transferred from their rearing location prior to release strayed at higher rates than those that were released from the rearing facility. Outplanting occurred for a variety of reasons ranging from supplementing fisheries to establishing new breeding populations, and often some fish returned to the rearing facility in addition to the release site. In many studies, a period of juvenile 'acclimation' (i.e., holding) near the release site appeared to improve homing to that site and reduce returns to the rearing facility. This has been reported for Chinook salmon (Dittman et al. 2010) coho salmon (Johnson et al. 2001) and steelhead (Clarke et al. 2010), among others. Notably, some studies have been equivocal about the homing benefit of acclimation (e.g., Kenaston et al. 2001; Clarke et al. 2011). The effectiveness of acclimation presumably depends on the location, the timing and duration of exposure, and the physiological condition and migration readiness of the juveniles being held.

Straying and wandering behaviors typically increased with outplanting distance within the natal watershed (e.g., Quinn et al. 1989; Insulander and Ragnarsson 2001; Gorsky et al. 2009). These behaviors also increased – sometimes by large increments – when juveniles were transferred to out-of-basin release locations (e.g., Lirette and Hooton 1988; Reisenbichler 1988; Labelle 1992; Hansen and Jonsson 1994). Similarly, outplanting into estuarine or saltwater sites typically produced more strays and reduced homing to the natal site (e.g., Hansen and Jonsson 1991; Candy and Beacham 2000).

5.7 JUVENILE TRANSPORTATION EFFECTS ON STRAYING

5.7.1 TRANSPORTATION STUDIES

We found about a dozen studies that have directly considered how barging or trucking juvenile salmon and steelhead downstream affects adult homing and straying in the Columbia River basin (Box 8). These studies mostly used juveniles that were collected after they had volitionally begun downstream migration (i.e., during the parr-smolt transformation). In this regard, these studies examined interrupted imprinting rather than incomplete imprinting (see Sections 4.2.1 and 4.2.2).

Box 8: Columbia River juvenile transportation studies with adult straying data

<u>Study</u>	<u>Year</u>	<u>Species</u>	<u>Experimental treatment*</u>
Ebel et al.	1973	CH, SH	Truck from Ice Harbor Dam to The Dalles reservoir (~200 km) or to the Bonneville tailrace (~300 km)
Slatick et al.	1975	CH, SH	Truck from Ice Harbor Dam to The Dalles reservoir (~200 km) or to the Bonneville tailrace (~300 km)
Vreeland et al.	1975	CO	Truck from L. White Salmon Hatchery to ~Col. R. mouth (~250 km)
Ebel	1980	CH, SH	Truck from L. Goose Dam to below Bonneville Dam (~400 km)
McCabe et al.	1983	CO	Truck, Barge from hatcheries to below Bonneville Dam (~40 km)
Bjornn & Ringe	1984	CH, SH	Truck from Snake River tributaries to Lower Granite Dam followed by Barge to lower Columbia River sites
Solazzi et al.	1991	CO	Truck from Cascade Hatchery to multiple release sites (various)
Bugert et al.	1997	FCH	Barge from Lyons Ferry Hatchery to Ice Harbor tailrace (~80 km)
Chapman et al.	1997	CH, SK	Truck and/or Barge from Priest Rapids and Wanapum dams to below Bonneville Dam (~430-460 km)
Keefer et al.	2008	CH, SH	Barge from Snake River dams to below Bonneville Dam (various)
Marsh et al.	2012	CH, SH	Barge from Lower Granite Dam to below Bonneville Dam (various)

*Note: control groups differed among studies

In general terms, there have been three eras of homing-related transportation research. In the earliest studies, prior to ~1990, the effects of barging was largely considered in relation to the relative proportions of barged versus in-river fish that returned to the juvenile collection site (see review by Ward et al. 1997). Straying assessments in these early studies was either anecdotal or based on recoveries of study fish at a limited number of collection sites other than the ‘home’ site. For this reason, the early studies almost certainly underestimated potential effects of trucking or barging on straying to non-natal sites. In the early Snake River and upper Columbia River studies, locations where strays were identified included a subsample of the hatcheries and

traps in the basin (mostly lower river) and some recovery sites in lower river fisheries and in the Columbia River upstream from the Hanford Reach. Some of the early studies reported no straying by transported fish (e.g., Ebel et al. 1973), while most others indicated that barged fish strayed at higher rates than in-river or on-site control groups (e.g., Vreeland et al. 1975; Ebel 1980; Bjornn and Ringe 1984). Estimates were typically qualitative rather than quantitative.

The second era of transportation research, mostly in the 1990s, used larger samples of marked fish, better experimental control groups, and somewhat more effort to identify strays (Box 8). The coho salmon transport study by Solazzi et al. (1991) was described above in Section 6.3.3 and primarily demonstrated that straying rate was positively related to downstream transport distance. The study by Chapman et al. (1997) evaluated a combination of trucking and barging experiments using sockeye salmon and spring Chinook salmon from the upper Columbia River. They found that transported juveniles – and especially trucked fish – fell back at dams as adults much more frequently than non-transport fish (i.e., their orientation appeared to be impaired). Transported fish were also more likely to be recovered as strays than were fish from the control groups; stray locations included several lower Columbia River hatcheries (Cowlitz, Cascade, Deschutes), though the recovery effort was limited. The study by Bugert et al. (1997) found that transported Chinook salmon from Lyons Ferry Hatchery strayed to sites outside the Snake River basin more than control groups. They also reported, however, that controls were more likely than transported fish to overshoot the hatchery upon return. Strays in this study were mostly recovered in the Hanford Reach of the Columbia River or adjacent hatcheries.

The third era of transportation studies was driven by the development of the PIT-tag interrogation system and, secondarily, by the large-scale adult radiotelemetry studies of the late 1990s and early 2000s. The widespread use of PIT tags in outmigrant juveniles allowed for the reconstruction of migration histories (including juvenile transportation histories) and some direct and indirect measures of straying based on adult detections. It was also possible to target previously PIT-tagged fish in the adult radiotelemetry studies, which allowed detailed evaluations of adult migration behaviors and final homing versus straying outcomes in relation to juvenile source and experience.

The most recent PIT-tag based straying study (Marsh et al. 2012) compared straying of Snake River adult spring–summer Chinook salmon and summer steelhead that were barged as juveniles to either just below Bonneville Dam or to a release site near the Columbia River estuary. The study found that steelhead that were barged to the estuary strayed at rates that were 1.61-1.98 times higher than for those that were barged to Bonneville Dam. Many of the barged fish from both groups were detected on in-stream PIT antennas in the Deschutes or John Day rivers, but eventually exited and continued to the Snake River. Marsh et al. (2012) reported considerably lower stray rates for Chinook salmon (0.3-3.7%) than for steelhead (4.3-8.5%). Straying sites in this study were limited to those with PIT-tag detection systems and there was no direct in-river control data reported. This study provided supporting evidence for increased straying with downstream transport distance and aligned with other studies showing substantial straying by Snake River steelhead into the Deschutes and John Day rivers (e.g., Hand and Olson 2003; Carmichael and Hoffnagle 2006; Ruzycki and Carmichael 2010).

The combined PIT and radiotelemetry study of Keefer et al. (2008b) showed that barged Snake River Chinook salmon and steelhead strayed at higher rates and fell back over dams far more often than those that had migrated in-river. Across the study years (adult returns 2000-2003), stray rates were 1.0% for in-river wild Chinook, 0.0% for in-river hatchery Chinook, 1.1% for barged wild Chinook, and 6.9% for barged hatchery Chinook. The estimates for steelhead were: 2.0% for in-river wild fish, 7.6% for in-river hatchery fish, 7.3% for barged wild fish, and 10.2% for barged hatchery fish. The Chinook estimates averaged higher than reported in Marsh et al. (2012), but steelhead estimates were generally comparable. Transported fish were also unaccounted for at higher rates (i.e., higher mortality or straying to unmonitored locations), and thus reported stray rates may underestimate the effect of transport on straying. As in the PIT-tag only studies, strays in the radiotelemetry research primarily entered lower and mid-Columbia River tributaries, and especially the Deschutes and John Day rivers. Concurrent and ongoing research by the Fish Passage Center's Comparative Survival Study (e.g., Berggren et al. 2005; DeHart 2007; Schaller et al. 2007; Tuomikoski et al. 2010, 2011) has corroborated both the higher straying by barged versus in-river fish and the tendency for straying into the Deschutes and John Day rivers. These reports have also reported some straying by Snake River fish into the upper Columbia River.

Overall, there is growing consensus that barging juvenile salmon and steelhead downstream increases the likelihood that they will stray as adults. The effect appears to be larger for summer steelhead than for spring–summer Chinook salmon and larger for hatchery fish than for wild fish. Patterns for fall Chinook salmon and sockeye salmon have not yet been well described, although both Chapman et al. (1997) and Bugert et al. (1997) provided some evidence that transported fish from these populations strayed more as well. The combined research indicate that there are unexplained differences in stray rates among years that are apparently related to river conditions in either (or both) the juvenile emigration year and the adult return year. In-season effects also appear likely, both related to juvenile collection date and adult return date. The juvenile timing effect presumably is related to physiological condition whereas the adult effect may be related to either fish condition (e.g., maturation status) or environmental cues (e.g., conditions that prompt thermoregulatory behaviors).

5.7.2 TRANSPORT-STRAYING MECHANISMS

The studies described above have provided some speculation on the mechanisms of how transport affects juvenile imprinting and adult homing, but considerable uncertainty remains. Assuming that the base effect is that transport interrupts sequential imprinting by juveniles, future evaluations are needed to identify the mechanisms responsible for the interruption. Hypotheses that are being tested or that have been proposed for testing include:

- transport speed effects, wherein rapid transport downstream in barges does not allow sufficient time for juvenile imprinting along the outmigration route or perception of distance during adult migration in transported individuals is biased compared to in-river individuals;

- transport timing effects, wherein diel or seasonal timing of transport is not well-matched to the juvenile's physiological readiness for imprinting (i.e., asynchrony between transport and smolt physiology);
- spatial effects, wherein the barge route (primarily in the shipping channel) does not allow juveniles to sample habitats needed for successful imprinting;
- in-barge effects, wherein stress, disease risk, endocrine physiology, toxin exposure, or other features of the barge environment (i.e., water circulation rates) reduce juvenile imprinting ability or opportunity;
- hatchery carryover effects, wherein a predisposition for straying by hatchery fish is increased by barging;
- among-population effects, wherein juveniles from some wild or hatchery populations are more likely to stray as adults if juveniles are transported;
- adult timing effects, wherein juvenile barging affects adult return migration date and consequently encountered river environment; or
- some combination of the above effects.

To date, the transport speed, transport timing, and spatial effects hypotheses have received little directed research attention, although there is some general agreement among managers and scientists that these factors likely play an important role in straying by barged fish. Controlled experiments at the scale required to differentiate these effects are probably necessary. However, relatively large samples would be needed to ensure sufficient adult returns to evaluate straying differences among treatments. Manipulating barge residence times and/or routes may be logistically demanding.

By comparison, several well-designed studies have evaluated the physiology (Barton et al. 1986; Maule et al. 1988; Congleton et al. 2000; Kelsey et al. 2002; Muir et al. 2006; Welker and Congleton 2009), disease susceptibility (Arkoosh et al. 2006), toxin exposure (Arkoosh et al. 2011), and sensory systems (e.g., Halvorsen et al. 2009) of smolts in barges versus their in-river counterparts. These studies have indicated that there are a complex combination of benefits (such as reduced exposure to some contaminants and diseases) and risks (such as increased stress) for barged juveniles. They also reported differences among hatchery and wild fish, and seasonal changes in a variety of smoltification and stress indicators. An understanding of how these patterns and processes affect adult homing behaviors will require considerably more work, including the ongoing effort to understand whether imprinting-related processes are affected by transport.

The hypotheses related to differences in straying related to carryover effects or to inherent differences among populations deserve additional attention. The studies by Hand and Olson (2003) and Carmichael and Hoffnagle (2006) clearly showed that some donor hatchery populations contributed more Snake River steelhead strays than others. It is likely that some

hatchery populations are barged at higher rates than others and it is also possible that not all groups respond to barging in the same way. Similarly, there are clear among-population differences in adult migration timing for both Chinook salmon and steelhead returning to the Snake River. Given the likelihood that some permanent straying is a result of adult behavioral responses to river environment, especially for steelhead, understanding such population-level effects may be helpful for predicting straying rates.

6.0 MODELING ADULT STRAYING BY SNAKE RIVER STEELHEAD

The final objective for this review was to estimate a range of potential impacts of straying to donor and recipient populations across a range of straying rates. The aim was to provide managers a context for evaluating the potential consequences of increased straying induced by transportation practices and how changes in straying rate would alter the number of spawners lost from or entering into populations of concern. For example, a goal was to answer questions such as “if new transportation practices reduced straying rate of barged steelhead by 50%, how many fewer Snake River steelhead would be expected to stray into the upper John Day river? How much would this reduce the proportion of out-of-basin spawners in this population?”. We developed a simple model described in section 6.1 and provide a general overview of scenarios and results in section 6.2.

6.1 MODEL DESCRIPTION

We used the model to develop a spreadsheet-based tool for modeling straying by Snake River steelhead, including the effects of juvenile barging. This tool was intended to be easily accessible (i.e., an Excel spreadsheet rather than specialized statistical software) with self-selected data inputs from recent (~10 years) agency data sources so that regional managers and other interested parties could test a variety of realistic straying scenarios. With input from USACE biologists and others involved with straying research in the Studies Review Working Group (SRWG), we developed the model described below. This tool is available at: <http://www.cnr.uidaho.edu/uiferl/Research.htm>

The basic model can be used to predict the number of Snake River steelhead that stray to sites outside the Snake River basin in a single year based on four input variables:

- the number of smolts that emigrated from the Snake River;
- the proportion of smolts transported (barged) downstream;
- the smolt-to-adult return rate (SAR) for each steelhead category (i.e., wild in-river, wild barged, hatchery in-river, hatchery-barged); and
- the estimated basin-wide stray rate (i.e., all strays to all locations).

A second model component allows users to select the stray rate from the Snake River into a single recipient population, such as the Deschutes or John Day River basins. This component can be used to estimate the approximate number of steelhead strays that enter these favored stray locations.

To simplify the modeling environment, we held several variables constant. These include: (1) the percentage of wild (13%) and hatchery (87%) steelhead smolts; and (2) adjustments to the SARs to account for harvest and other adult ‘loss’ between Bonneville Dam and Lower Granite Dam. The latter were calculated using recent mean adult conversion rates from Bonneville to Lower Granite (i.e., the proportion that migrated from Bonneville Dam to Lower Granite Dam,

as reported by the Fish Passage Center) and were: 0.794 (wild, in-river), 0.697 (wild, barged), 0.776 (hatchery, in-river) and 0.730 (hatchery, barged).

The model spreadsheet uses pull-down menus where users can select each of the input data types in the bullets above. The source data were collected from the Fish Passage Center website (smolt index, transport proportion), from the Comparative Survival Study (SARs, Tuomikoski et al. 2011), and from the straying research described in previous sections, especially Ruzycki and Carmichael (1010) and Keefer et al. (2008b). Users can also input recent estimates of native steelhead escapement into the Deschutes and John Day rivers for the single recipient population component (data source: 2010 ODFW Mid-Columbia Recovery Plan, Appendix B). We consider the stray rate data the least reliable of these inputs because straying has received relatively limited research attention. Therefore, the model allows users to input from a range of potential stray rates.

6.2 EXAMPLES OF MODEL OUTPUTS

6.2.1 BASIN-WIDE STRAY RATE ESTIMATES

Below we present model outputs for the total strays lost from the Snake River donor population across a range of realistic values. Figures 10-12 show estimates of ‘total strays’ lost from the Snake River steelhead donor population that entered all recipient populations. Estimates were generated for each combination of hatchery, wild, barged, and in-river fish. Each figure uses mean values for three of the input variables while varying inputs from a fourth variable. Note

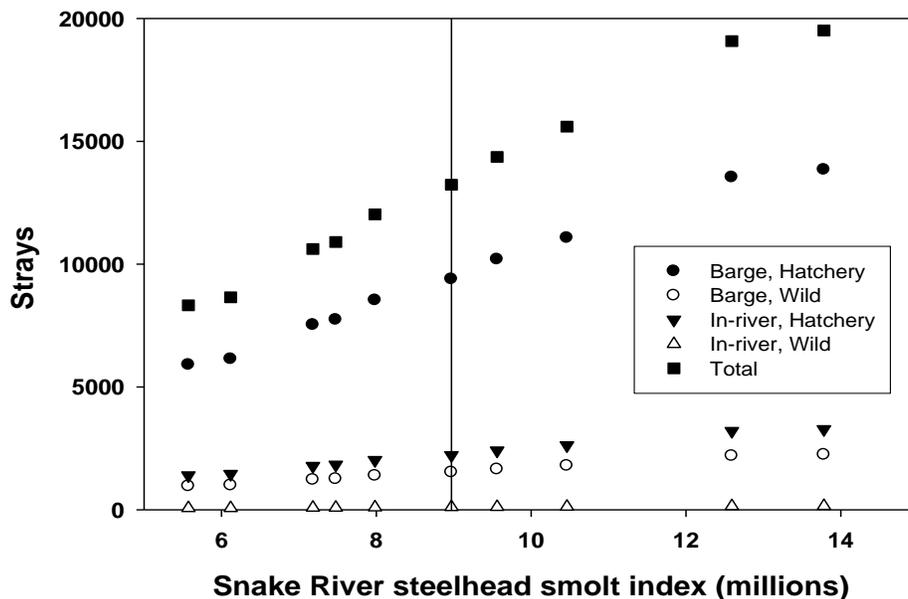


Figure 10. Estimated numbers of Snake River steelhead strays across a range of smolt abundance values at Lower Granite Dam. Transport (barge) proportion was held constant at 0.64. SARs for each category were held constant at 1.62 (hatchery, barge), 2.16 (wild, barge), 0.86 (hatchery, in-river), and 1.08 (wild, in-river). Total stray rates were held constant at 8.5% (hatchery, barge), 6.6% (wild, barge), 7.1% (hatchery, in-river), and 1.8% (wild, in-river). The stray values were derived from Keefer et al. (2008b).

that a large number of additional estimates are possible; these were selected to give a general overview of model outputs and the relative sensitivity of the estimates to the different input variables.

In most scenarios, transported hatchery strays were the most abundant group, reflecting the overall demographics of the Snake River populations. Total estimates of strays were sensitive to the total number of steelhead smolts at Lower Granite Dam, with estimates of ~8,000 following years with low smolt production to nearly 20,000 when smolt abundance was near recent highs (Figure 10).

When we held smolt abundance to the recent mean of ~9 million and varied barge rate across the range of recent values (~0.40-0.95), the estimated total number of steelhead strays ranged between ~10,000 and ~17,000 (Figure 11). As transport proportion increased, the number of strays from in-river groups declined, as would be expected.

Total stray estimates were also quite sensitive to SAR rates (Figure 12). Lower SARs mean fewer adults return to the Columbia River basin, and hence there are fewer available to stray. The estimates in Figure 12 varied SARs separately for each group (hatchery, wild, transport, in-river) to show the number of strays across the range of estimates available for each of these categories. In the model, each of these SARs is an independent input.

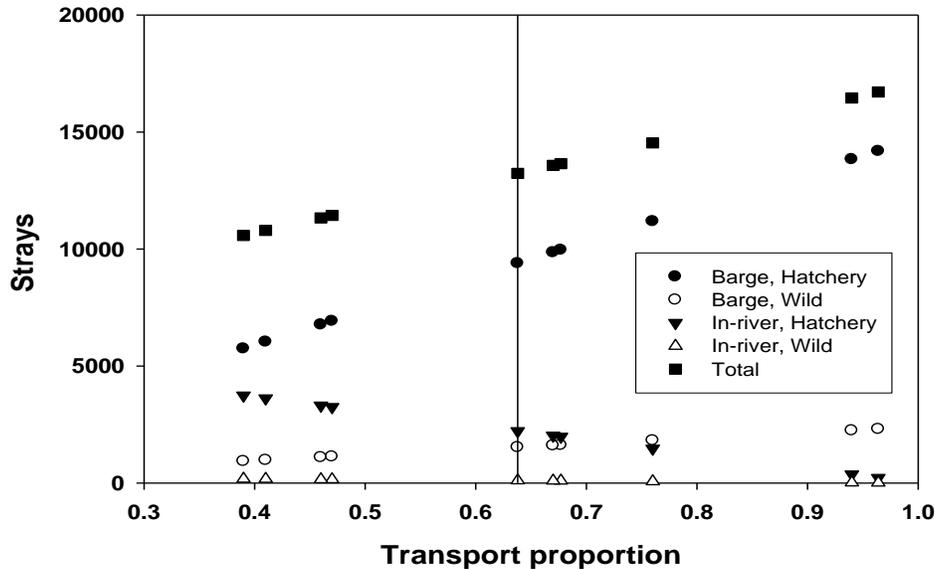


Figure 11. Estimated numbers of Snake River steelhead strays across a range of transport proportion values. The smolt abundance index was held constant at ~9 million. SARs for each category were held constant at 1.62 (hatchery, barge), 2.16 (wild, barge), 0.86 (hatchery, in-river), and 1.08 (wild, in-river). Total stray rates were held constant at 8.5% (hatchery, barge), 6.6% (wild, barge), 7.1% (hatchery, in-river), and 1.8% (wild, in-river). The stray values were derived from Keefer et al. (2008b).

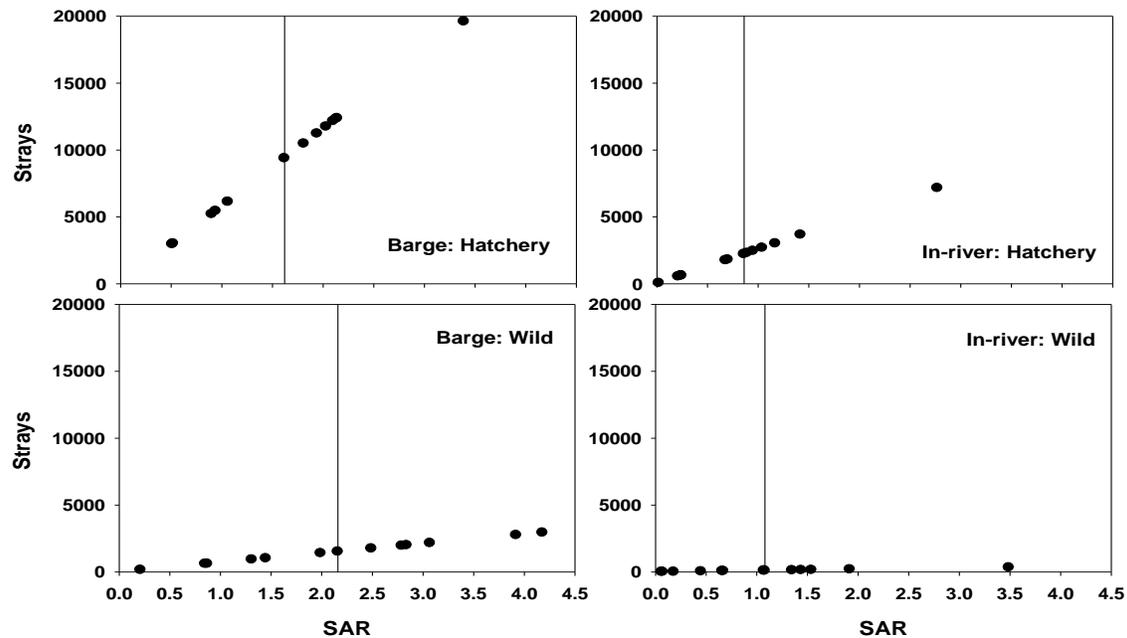


Figure 12. Estimated numbers of Snake River steelhead strays across a range of SAR values. The smolt abundance index was held constant at ~9 million. Transport (barge) proportion was held constant at 0.64. Total stray rates were held constant at 8.5% (hatchery, barge), 6.6% (wild, barge), 7.1% (hatchery, in-river), and 1.8% (wild, in-river). The stray values were derived from Keefer et al. (2008b).

6.2.2 SINGLE RECIPIENT POPULATION ESTIMATES

Figure 13 shows an amalgamation of model estimates from the single recipient population component of the spreadsheet model. This element of the model allows users to estimate the number of steelhead strays into single recipient basins, in this case the John Day River, and to compare the number of strays to the number of natives (users can input native population estimates from recent years). We define this ratio as the proportion of out-of-basin spawners ($p_{OBS} = \text{strays}/(\text{strays}+\text{natives})$), which is directly analogous to the proportion of hatchery-origin spawners (p_{HOS}) in mixed native and hatchery spawning groups. Some combinations of input variables result in Snake River strays outnumbering ‘native’ spawners. This is most likely to occur when Snake River smolt abundance is high, many fish are barged, SARs are above average, and native abundance in the recipient population is relatively low. The escapement and survey data described by Hand and Olson (2003), Carmichael and Hoffnagle (2006), and Ruzycki and Carmichael (2010) suggest that such outcomes are plausible in some years.

Refining this model component will require more accurate estimates of stray rates from the Snake River into single recipient populations. Currently, such information is limited, with the partial exception of the Deschutes and John Day river basins. Considerable uncertainty remains about the absolute numbers of breeding straying and about where strays are distributed within the

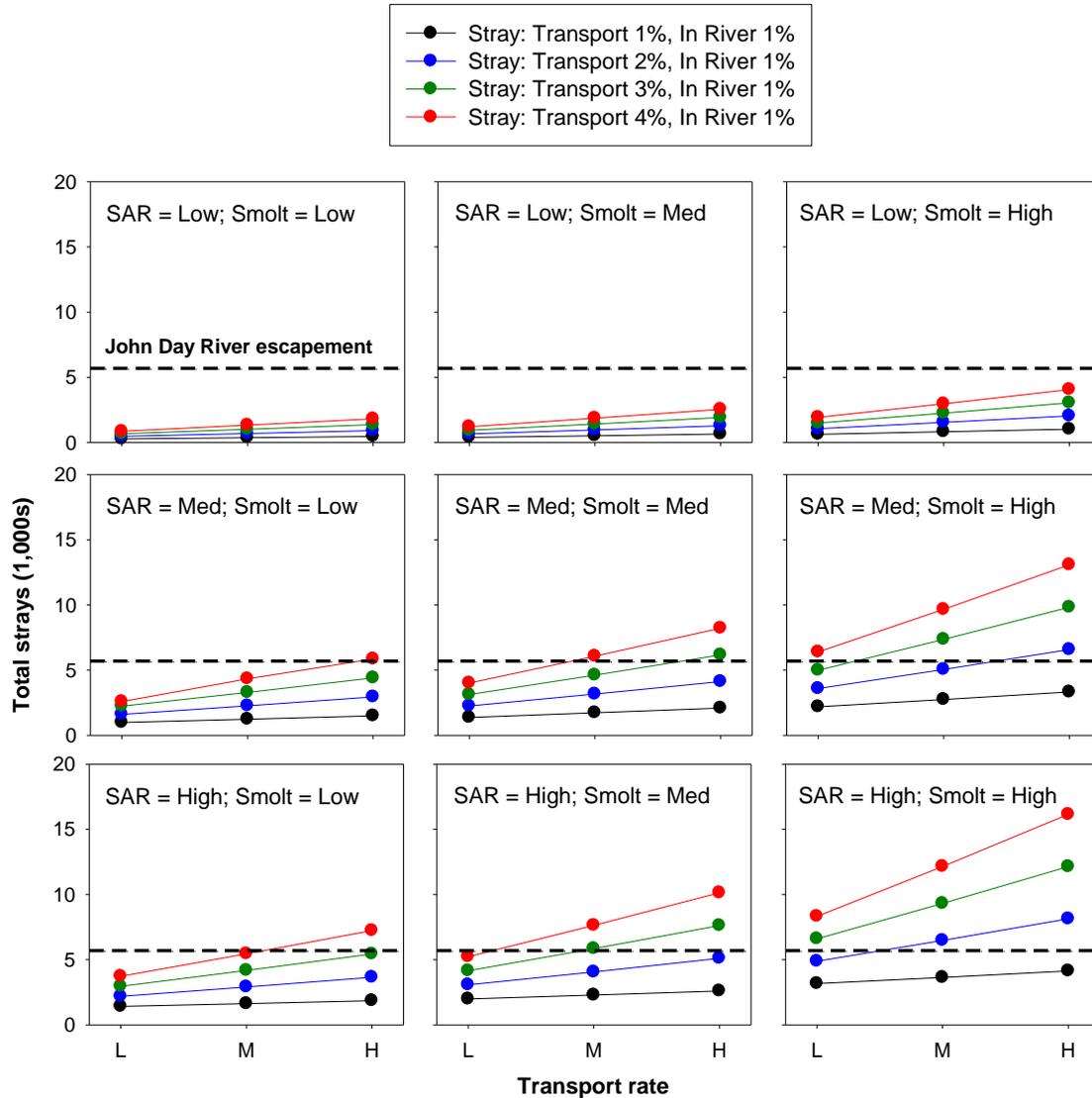


Figure 13. Estimated numbers of Snake River steelhead strays that enter a single recipient system using four combinations of stray rates for barged and in-river fish (legend at top). The nine panels show the 3×3 combinations of smolt abundance (low to high, from right to left columns), SARs (low to high, from top to bottom rows), and smolt transport rate (low to high on x-axis of each panel). The horizontal dashed line represents the recent mean ‘native’ escapement to the John Day River basin.

recipient river systems. Nonetheless, both the reviewed literature and the Snake River steelhead straying model indicate that it is possible for strays from the large Snake River population to numerically overwhelm small recipient populations.

The information presented here should allow managers to begin consider the potential effects of efforts to reduce straying by barged fish. The simple numerical model results in Figure 14 (same as Figure 1) show how the proportion of out-of-basin strays (pOBS) varies with the three main inputs: donor population size, recipient population size, and stray rate. This type of model, which is a simplification and generalization of the Snake River steelhead straying model, is

useful as a heuristic tool. It can facilitate basic comparisons of different management alternatives or preferred outcomes related to straying by barged fish.

For example, managers may set a target of 1% straying into the John Day River. The four panels in Figure 14 show the proportional abundance of strays across a realistic range of both donor and recipient population sizes given a 1% donor population stray rate (the solid line). Alternately, managers may want to estimate the effect of reducing straying by barged fish from 3% to 1%, which is the difference between the dotted and solid lines in Figure 14. A third example is that managers may set a target of the proportion of strays in the recipient population, such as: $\text{strays}/\text{strays}+\text{natives} = 0.2$. To achieve this outcome, stray rates would need to be reduced far below 1% for smaller recipient population sizes.

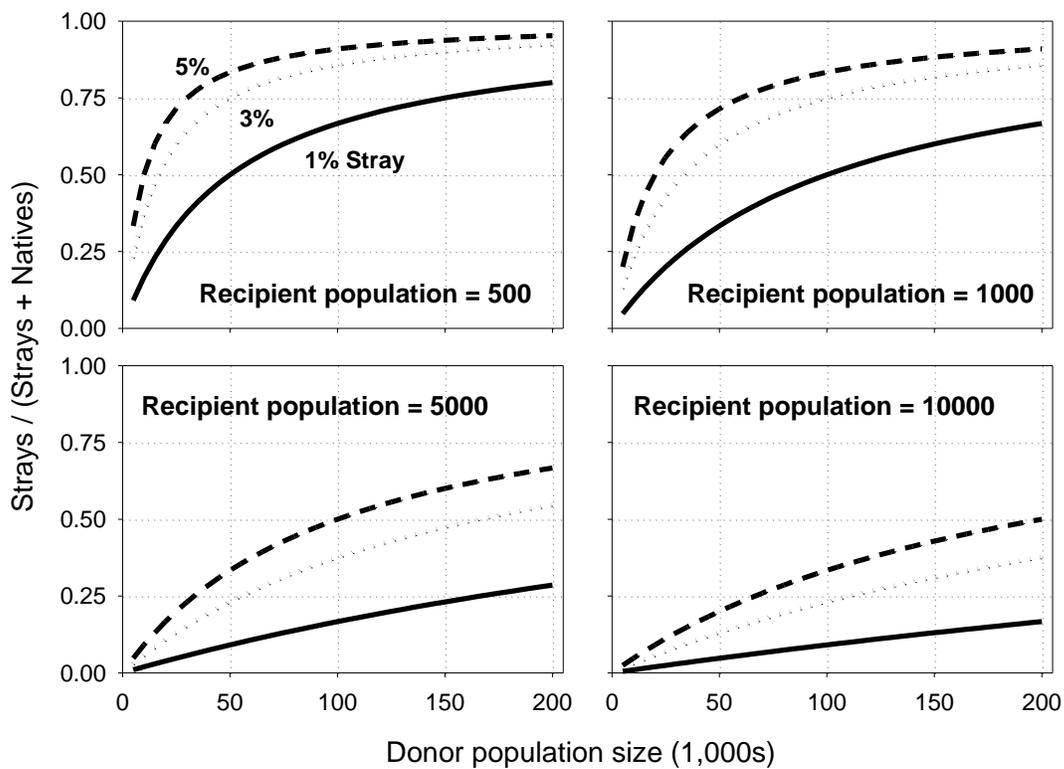


Figure 14. Examples of the proportions of adult strays that spawn with a local recipient population (strays/(strays+natives)) as estimated using four recipient population sizes (four panels: 500, 1,000, 5,000, or 10,000 fish), a range of donor population size (0-200,000), and three donor stray rates: 1% (solid line), 3% (dotted line), and 5% (dashed line). Small recipient populations can be numerically dominated by strays when the donor population is large, even when stray rates are low. (Note: same as Figure 1).

The results of this review and modeling exercise suggest that transportation effects on adult straying can have large effects on both donor and local recipient populations, and that the effects could potentially be reduced through alternative transportation practices. Use of population-specific modeling as presented in the spreadsheet tool, pOBS, and similar quantitative metrics to evaluate effects of varying stray rate on specific populations of interest should help managers assess the relative costs and benefits of potential alternative transportation scenarios.

7.0 LITERATURE CITED

- Anderson, J. H., and T. P. Quinn. 2007. Movements of adult coho salmon (*Oncorhynchus kisutch*) during colonization of newly accessible habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 64:1143-1154.
- Araki, H., R. S. Waples, W. R. Ardren, B. Cooper, and M. S. Blouin. 2007. Effective population size of steelhead trout: influence of variance in reproductive success, hatchery programs, and genetic compensation between life-history forms. *Molecular Ecology* 16:953-966.
- Arkoosh, M. R., A. N. Kagley, B. F. Anulacion, D. A. Boylen, B. P. Sandford, F. J. Loge, L. J. Johnson, and T. K. Collier. 2006. Disease susceptibility of hatchery Snake River spring-summer Chinook salmon with different juvenile migration histories in the Columbia River. *Journal of Aquatic Animal Health* 18:223-231.
- Arkoosh, M. R., S. Strickland, A. Van Gaest, G. M. Ylitalo, L. Johnson, G. K. Yanagida, T. K. Collier, and J. P. Dietrich. 2011. Trends in organic pollutants and lipids in juvenile Snake River spring Chinook salmon with different outmigrating histories through the lower Snake and middle Columbia rivers. *Science of the Total Environment* 409:5086-5100.
- Arnsberg, B. D., D. S. Kellar, and M. A. Tuell. 2007. Nez Perce tribal hatchery monitoring and evaluation of fall Chinook salmon supplementation in the Clearwater River subbasin: annual report 2003. Nez Perce Tribe, Orofino, Idaho.
- Baker, C., J. C. Graham, and S. R. Narum. 2008. Origin of out of basin stray fall Chinook salmon in the Deschutes River, Oregon. Final Report to the Pacific Salmon Commission by Confederated Tribes of the Warm Springs Reservation of Oregon and Columbia River Inter-Tribal Fish Commission.
- Baldwin, D. H., J. F. Sandahl, J. S. Labenia, and N. L. Scholz. 2003. Sublethal effects of copper on coho salmon: impacts on non-overlapping receptor populations in the peripheral olfactory nervous system. *Environmental Toxicology and Chemistry* 22:2266-2274.
- Baldwin, D. H., C. P. Tatara, and N. L. Scholz. 2011. Copper-induced olfactory toxicity in salmon and steelhead: extrapolation across species and rearing environments. *Aquatic Toxicology* 101:295-297.
- Bams, R. A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). *Journal of the Fisheries Research Board of Canada* 33:2716-2725.
- Bandoh, H., I. Kida, and H. Ueda. 2011. Olfactory responses to natal stream water in sockeye salmon by BOLD fMRI. *PLoS One* 6:e16051.

- Bargmann, C. I. 1997. Olfactory receptors, vomeronasal receptors, and the organization of olfactory information. *Cell* 90:585-587.
- Barry, T. P., M. J. Unwin, J. A. Malison, and T. P. Quinn. 2005. Free and total cortisol levels in semelparous and iteroparous Chinook salmon. *Journal of Fish Biology* 59:1673-1676.
- Bartron, M. L., D. R. Swank, E. S. Rutherford, and K. T. Scribner. 2004. Methodological bias in estimates of strain composition and straying of hatchery-produced steelhead in Lake Michigan tributaries. *North American Journal of Fisheries Management* 24:1288-1299.
- Becker, L. A., M. A. Pascual, and N. G. Basso. 2007. Colonization of the Southern Patagonian Ocean by exotic Chinook salmon. *Conservation Biology* 21:1347-1352.
- Beckman, B. R., D. A. Larsen, and W. W. Dickhoff. 2003. Life history plasticity in Chinook salmon: relation of size and growth rate to autumnal smolting. *Aquaculture* 222:149-165.
- Bentzen, P., J. B. Olsen, J. E. McLean, T. R. Seamons, and T. P. Quinn. 2001. Kinship analysis of Pacific salmon: Insights into mating, homing, and timing of reproduction. *Journal of Heredity* 92:127-136.
- Berggren, T., H. Franzoni, L. Bashram, P. Wilson, H. Schaller, C. Petrosky, E. Weber, R. Boyce, and N. Bouwes. 2005. Comparative survival study (CSS) of PIT-tagged spring/summer Chinook and PIT-tagged summer steelhead. 2005 Annual Report. BPA Contract #19960200. 98 pp.
- Berman, C. H., and T. P. Quinn. 1991. Behavioural thermoregulation and homing by spring Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *Journal of Fish Biology* 39:301-312.
- Bjornn, T. C., and R. R. Ringe. 1984. Homing of hatchery salmon and steelhead allowed a short-distance voluntary migration before transport to the lower Columbia River. Final Report of Idaho Cooperative Fish and Wildlife Research Unit to National Marine Fisheries Service, Seattle, Washington.
- Bjørnsson, B. T., S. O. Stefansson, and S. D. McCormick. 2011. Environmental endocrinology of salmon smoltification. *General and Comparative Endocrinology* 170:290-298.
- Blankenship, H. L., and G. W. Mendel. 1993. Upstream passage, spawning, and stock identification of fall Chinook salmon in the Snake River, 1992. Annual Report FY 92-93 of Washington Department of Fisheries to Bonneville Power Administration.
- Blankenship, H. L., and G. W. Mendel. 1997. Upstream passage, spawning, and stock identification of fall Chinook salmon in the Snake River, 1992 and 1993. Final Report of Washington Department of Fisheries to Bonneville Power Administration, Project #199204600.

- Boggs, C. T., M. L. Keefer, C. A. Peery, T. C. Bjornn, and L. C. Stuehrenberg. 2004. Fallback, reascension and adjusted fishway escapement estimates for adult Chinook salmon and steelhead at Columbia and Snake River dams. *Transactions of the American Fisheries Society* 133:932-949.
- Bracis, C., and J. J. Anderson. 2012. An investigation of the geomagnetic imprinting hypothesis for salmon. *Fisheries Oceanography* 21:170-181.
- Brannon, E. L. 1982. Orientation mechanisms of homing salmonids. Pages 219-227 *in* E. L. Brannon and E. O. Salo, editors. *Salmon and trout migratory behavior symposium*. University of Washington. Seattle, Washington.
- Brannon, E. L., M. S. Powell, T. P. Quinn, and A. Talbot. 2004. Population structure of Columbia River basin Chinook salmon and steelhead trout. *Reviews in Fisheries Science* 12:99-232.
- Brenner, R. E., S. D. Moffitt, and W. S. Grant. 2012. Straying of hatchery salmon in Prince William Sound, Alaska. *Environmental Biology of Fishes* 94:179-195.
- Bryant, M. D., B. J. Frenette, and S. J. McCurdy. 1999. Colonization of a watershed by anadromous salmonids following the installation of a fish ladder in Margaret Creek, Southeast Alaska. *North American Journal of Fisheries Management* 19:1129-1136.
- Bumgarner, J. D., and J. T. Dedloff. 2011. Lyons Ferry Complex hatchery evaluation: summer steelhead annual report 2008 and 2009 run year. Washington Department of Fish and Wildlife, Olympia, Washington.
- Bugert, R. M., G. W. Mendel, and P. R. Seidel. 1997. Adult returns of subyearling and yearling fall Chinook salmon released from a Snake River hatchery or transported downstream. *North American Journal of Fisheries Management* 17:638-651.
- Burger, C. V., J. E. Finn, and L. Holland-Bartels. 1995. Patterns of shoreline spawning by sockeye salmon in a glacially turbid lake: evidence for subpopulation differentiation. *Transactions of the American Fisheries Society* 124:1-15.
- Burger, C. V., W. J. Spearman, and M. A. Cronin. 1997. Genetic differentiation of sockeye salmon subpopulations from a geologically young Alaskan lake system. *Transactions of the American Fisheries Society* 126:926-938.
- Busby, P. J., T. C. Wainwright, E. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27.

- Candy, J. R., and T. D. Beacham. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged Chinook salmon (*Oncorhynchus tshawytscha*) populations. *Fisheries Research* 47:41-56.
- Carmichael, R. W., and T. L. Hoffnagle. 2006. Hatchery steelhead straying in the Deschutes River basin. *The Osprey* 55:14-17.
- Carruth, L. L., R. E. Jones, and D. O. Norris. 2000. Elevation of plasma cortisol during the spawning migration of a landlocked kokanee salmon (*Oncorhynchus nerka*). *Comparative Biochemistry and Physiology C* 127:123-131.
- Carruth, L. L., R. E. Jones, and D. O. Norris. 2002. Cortisol and Pacific salmon: a new look at the role of stress hormones in olfaction and home-stream navigation. *Integrative and Comparative Biology* 42:574-581.
- Carton, A. G., and J. C. Montgomery. 2003. Evidence of a rheotactic component in the odour search of freshwater eels. *Journal of Fish Biology* 62:501-516.
- Chapman, D., C. Carlson, D. Weitkamp, G. Matthews, J. Stevenson, and M. Miller. 1997. Homing in sockeye and Chinook salmon transported around part of the smolt migration route in the Columbia River. *North American Journal of Fisheries Management* 17:101-113.
- Chilcote, M. W. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 60:1057-1067.
- Chilcote, M. W., K. W. Goodson, and M. R. Falcy. 2011. Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences* 68:511-522.
- Chilcote, M. W., S. A. Leider, and J. J. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Transactions of the American Fisheries Society* 115:726-735.
- Chittenden, C. M., S. Sura, K. G. Butterworth, K. F. Cubitt, N. Plantalech Manel-la, S. Balfry, F. Økland, and R. S. McKinley. 2008. Riverine, estuarine and marine migratory behaviour and physiology of wild and hatchery-reared coho salmon *Oncorhynchus kisutch* (Walbaum) smolts descending the Campbell River, BC, Canada. *Journal of Fish Biology* 72:614-628.
- Clarke, L. R., M. W. Flesher, T. A. Whitesel, G. R. Vonderohe, and R. W. Carmichael. 2010. Postrelease performance of acclimated and directly released hatchery summer steelhead into Oregon tributaries of the Snake River. *North American Journal of Fisheries Management* 30:1098-1109.

- Clarke, L. R., M. W. Flesher, S. M. Warren, and R. W. Carmichael. 2011. Survival and straying of hatchery steelhead following forced or volitional release. *North American Journal of Fisheries Management* 31:116-123.
- Congleton, J. L., W. J. LaVoie, C. B. Schreck, and L. E. Davis. 2000. Stress indices in migrating juvenile Chinook salmon and steelhead of wild and hatchery origin before and after barge transportation. *Transactions of the American Fisheries Society* 129:946-961.
- Connor, W. P., and A. P. Garcia. 2006. Prespawning movements of wild and hatchery fall Chinook salmon adults in the Snake River. *Transactions of the American Fisheries Society* 135:297-305.
- Connor, W. P., A. R. Marshall, T. C. Bjornn, and H. L. Burge. 2001. Growth and long-range dispersal by wild subyearling spring and summer Chinook salmon in the Snake River basin. *Transactions of the American Fisheries Society* 130:1070-1076.
- Cooper, J. C., and A. D. Hasler. 1976. Electrophysiological studies of morpholine-imprinted coho salmon (*Oncorhynchus-kisutch*) and rainbow trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada* 33:688-694.
- Cooper, J. C., A. T. Scholz, R. M. Horrall, A. D. Hasler, and D. M. Madison. 1976. Experimental confirmation of olfactory hypothesis with homing, artificially imprinted coho salmon (*Oncorhynchus-kisutch*). *Journal of the Fisheries Research Board of Canada* 33:703-710.
- Correa, C., and M. R. Gross. 2008. Chinook salmon invade southern South America. *Biological Invasions* 10:615-639.
- Courtenay, S. C. 1989. Learning and memory of chemosensory stimuli by under-yearling coho salmon *Oncorhynchus kisutch* (Walbaum). Ph.D. thesis, Department of Zoology, University of British Columbia.
- Courtenay, S. C., T. P. Quinn, H. M. C. Dupuis, C. Groot, and P. A. Larkin. 1997. Factors affecting the recognition of population-specific odours by juvenile coho salmon. *Journal of Fish Biology* 50:1042-1060.
- Courtenay, S. C., T. P. Quinn, H. M. C. Dupuis, C. Groot, and P. A. Larkin. 2001. Discrimination of family-specific odours by juvenile coho salmon: roles of learning and odour concentration. *Journal of Fish Biology* 58:107-125.
- Cram, J. M., C. E. Torgersen, R. S. Klett, G. R. Pess, D. May, T. N. Pearsons, and A. H. Dittman. 2012. Tradeoffs between homing and habitat quality for spawning site selection by hatchery-origin Chinook salmon. *Environmental Biology of Fishes* 94:
- Crawford, E., M. Schuck, and M. Herr. 2012. Asotin Creek salmonid assessment 2011 annual report. Report by Washington Department of Fish and Wildlife for Bonneville Power Administration. BPA Project # 2002-053-00.

- Crawford, S. S. 2001. Salmonine introductions to the Laurentian Great Lakes: an historical review and evaluation of ecological effects. Canadian Special Publication of Fisheries and Aquatic Sciences 132.
- Crespi, B. J., and R. Teo. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. *Evolution* 56:1008-1020.
- Dat, C. G., P. H. LeBlond, K. A. Thompson, and W. J. Ingraham Jr. 1995. Computer simulations of homeward migrating Fraser River sockeye salmon: is compass orientation a sufficient direction-finding mechanism in the north-east Pacific Ocean? *Fisheries Oceanography* 4:209-219.
- DeBose, J. L., and G. A. Nevitt. 2008. The use of odors at different spatial scales: comparing birds with fish. *Journal of Chemical Ecology* 34:867-881.
- DeHart, M. 2007. Associations between upstream migration success and smolt outmigration history for returning adult Snake River-origin hatchery and wild summer steelhead. Fish Passage Center Memorandum, 18 January 2007.
- Dennis, B. 2002. Allee effects in stochastic populations. *Oikos* 96:389-401.
- Dempson, J. B., V. A. Pepper, G. Furey, M. Bloom, T. Nicholls, and G. Hoskins. 1999. Evaluation of an alternative strategy to enhance salmon populations: cage rearing wild smolts from Conne River, Newfoundland. *ICES Journal of Marine Science* 56:422-432.
- Dickhoff, W. W. 1989. Salmonids and annual fishes: death after sex. Pages 253-266 in M. P. Schreibman and C. G. Scanes, editors. *Development, maturation, and senescence of neuroendocrine systems: a comparative approach*. Academic Press, New York.
- Dickhoff, W. W., and C. Sullivan. 1987. Involvement of the thyroid gland in smoltification, with special reference to metabolic and developmental processes. *American Fisheries Society Symposium* 1:197-210.
- Dittman, A. H., D. May, D. A. Larsen, M. L. Moser, M. Johnston, and D. Fast. 2010. Homing and spawning site selection by supplemented hatchery- and natural-origin Yakima River spring Chinook salmon. *Transactions of the American Fisheries Society* 139:1014-1028.
- Dittman, A. H., and T. P. Quinn. 1996. Homing in Pacific salmon: mechanisms and ecological basis. *Journal of Experimental Biology* 199:83-91.
- Dittman, A. H., T. P. Quinn, and G. A. Nevitt. 1996. Timing of imprinting to natural and artificial odors by coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 53:434-442.

- Dittman, A. H., T. P. Quinn, G. A. Nevitt, B. Hacker, and D. R. Storm. 1997. Sensitization of olfactory guanylyl cyclase to a specific imprinted odorant in coho salmon. *Neuron* 19:381-389.
- Døving, K. B., and O. B. Stabell. 2003. Trails in open waters: sensory cues in salmon migration. Pages 39-52 in S. P. Collin and N. J. Marshall, editors. *Sensory processing in aquatic environments*. Springer-Verlag, New York.
- Døving, K. B., H. Westerberg, and P. B. Johnsen. 1985. Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1658-1667.
- Dukes, J. P., R. Deaville, M. W. Bruford, A. F. Youngson, and W. C. Jordan. 2004. Odorant receptor gene expression changes during the parr-smolt transformation in Atlantic salmon. *Molecular Ecology* 13:2851-2857.
- Ebel, W. J., D. L. Park, and R. C. Johnsen. 1973. Effects of transportation on survival and homing of Snake River Chinook salmon and steelhead trout. *Fishery Bulletin* 71:549-563.
- Ebel, W. J. 1980. Transportation of Chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo Gairdneri*, smolts in the Columbia River and effects on adult returns. U.S. National Marine Fishery Service *Fishery Bulletin* 78:491-505.
- Fitzpatrick, M. S., G. van der Kraak, and C. B. Schreck. 1986. Profiles of plasma sex steroids and gonadotropin in coho salmon, *Oncorhynchus kisutch*, during final maturation. *General and Comparative Endocrinology* 62:437-451.
- Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries* 6:379-416.
- Fleming, I. A., and M. R. Gross. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. *Ecological Applications* 3:230-245.
- Fleming, I. A., K. Hindar, I. B. Mjølnærod, B. Jonsson, T. Balstad, and A. Lamberg. 2000. Lifetime success and interactions of farm salmon invading a native population. *Proceedings of the Royal Society of London Series B-Biological Sciences* 267:1517-1523.
- Fleming, I. A., and J. D. Reynolds. 2004. Salmon breeding systems. Pages 264-294 in A. P. Hendry and S. C. Stearns, editors. *Evolution illuminated: salmon and their relatives*. Oxford University Press, New York.
- Frank, K. T., and D. Brickman. 2000. Allee effects and compensatory population dynamics within a stock complex. *Canadian Journal of Fisheries and Aquatic Sciences* 57:513-517.

- Gallinat, M. P, and L. A. Ross. 2011. Tucannon River spring Chinook salmon hatchery evaluation program: 2010 annual report. Washington Department of Fish and Wildlife, Olympia, Washington.
- Garcia, A. P., W. P. Connor, D. J. Milks, S. J. Rocklage, and R. K. Steinhorst. 2004. Movement and spawner distribution of hatchery fall Chinook salmon adults acclimated and released as yearlings at three locations in the Snake River basin. *North American Journal of Fisheries Management* 24:1134-1144.
- Geist, D. R., and D. D. Dauble. 1998. Redd site selection and spawning habitat use by fall Chinook salmon: the importance of geomorphic features in large rivers. *Transactions of the American Fisheries Society* 22:655-669.
- Gilk, S. E., I. A. Wang, C. L. Hoover, W. H. Smoker, S. G. Taylor, A. K. Gray, and A. J. Gharrett. 2004. Outbreeding depression in hybrids between spatially separated pink salmon, *Oncorhynchus gorbuscha*, populations: marine survival, homing ability, and variability in family size. *Environmental Biology of Fishes* 69:287-297.
- Gonia, T. M., M. L. Keefer, T. C. Bjornn, C. A. Peery, D. H. Bennett, and L. C. Stuehrenberg. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. *Transactions of the American Fisheries Society* 135:408-419.
- Gorsky, D., J. Trial, J. Zydlewski, and J. McCleave. 2009. The effects of smolt stocking strategies on migratory path selection of adult Atlantic salmon in the Penobscot River, Maine. *North American Journal of Fisheries Management* 29:949-957.
- Griffith, J. N., A. P. Hendry, and T. P. Quinn. 1999. Straying of adult sockeye salmon, *Oncorhynchus nerka*, entering a non-natal hatchery. *Fishery Bulletin* 97:713-716.
- Groot, C., and L. Margolis. 1991. Pacific salmon life histories. University of British Columbia Press. Vancouver, British Columbia.
- Groot, C., T. P. Quinn, and T. J. Hara. 1986. Responses of migrating adult sockeye salmon (*Oncorhynchus nerka*) to population-specific odors. *Canadian Journal of Zoology* 64:926-932.
- Gunnerød, T. B., N. A. Hvidsten, and T. G. Heggberget. 1988. Open sea releases of Atlantic salmon smolts, *Salmo salar*, in central Norway, 1973-83. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1340-1345.
- Halvorsen, M. B., L. E. Wysocki, C. M. Stehr, D. H. Baldwin, D. R. Chicoine, N. L. Scholz, and A. N. Popper. 2009. Barging effects on sensory systems of Chinook salmon smolts. *Transactions of the American Fisheries Society* 138:777-789.

- Hamann, E. J., and B. P. Kennedy. 2012. Juvenile dispersal affects straying behaviors of adults in a migratory population. *Ecology* 93:733-740.
- Hand, D., and D. Olson. 2003. Steelhead returns to Warm Springs National Fish Hatchery, 1978-2003. U.S. Fish and Wildlife Service, Vancouver, Washington.
- Hansen, L. P., and B. Jonsson. 1991. The effect of timing of Atlantic salmon smolt and post-smolt release on the distribution of adult return. *Aquaculture* 98:61-67.
- Hansen, L. P., and B. Jonsson. 1994. Homing of Atlantic salmon: effects of juvenile learning on transplanted post-spawners. *Animal Behaviour* 47:220-222.
- Hansen, L. P., N. Jonsson, and B. Jonsson. 1993. Oceanic migration in homing Atlantic salmon. *Animal Behaviour* 45:927-941.
- Hara, T. J., K. Ueda, and A. Gorbman. 1965. Electroencephalograph studies of homing salmon. *Science* 149:884-885.
- Hard, J. J., and W. R. Heard. 1999. Analysis of straying variation in Alaskan hatchery Chinook salmon (*Oncorhynchus tshawytscha*) following transplantation. *Canadian Journal of Fisheries and Aquatic Sciences* 56:578-589.
- Harden Jones, F. R. 1968. *Fish Migration*. Edward Arnold Ltd., London.
- Hasler, A. D. 1966. *Underwater guideposts*. University of Wisconsin Press. Madison, Wisconsin.
- Hasler, A. D., and A. T. Scholz. 1983. *Olfactory imprinting and homing in salmon*. Springer-Verlag, Berlin.
- Hasler, A. D., A. T. Scholz, and R. M. Horrall. 1978. Olfactory imprinting and homing in salmon. *American Scientist* 66:347-355.
- Hasler, A. D., and W. J. Wisby. 1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. *The American Naturalist* 85:223-238.
- Hayes, M. C., and R. W. Carmichael. 2002. Salmon restoration in the Umatilla River: a study of straying and risk containment. *Fisheries* 27(10):10-19.
- Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 313-393 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. University of British Columbia, Vancouver, British Columbia.
- Heard, W. R. 1996. Sequential imprinting in Chinook salmon: is it essential for homing fidelity? *Bulletin of National Research Institute of Aquaculture Suppl* 2:59-64.

- Heggberget, T. G., N. A. Hvidsten, T. B. Gunnerød, and P. I. Møkkelgjerd. 1991. Distribution of adult recaptures from hatchery-reared Atlantic salmon (*Salmo salar*) smolts released in and off-shore of the River Surna, western Norway. *Aquaculture* 98:89-96.
- Hendry, A. P. 2001. Adaptive divergence and the evolution of reproductive isolation in the wild: an empirical demonstration using introduced sockeye salmon. *Genetica* 113:515-534.
- Hendry, A. P., V. Castric, M. T. Kinnison, and T. P. Quinn. 2004. The evolution of philopatry and dispersal: homing versus straying in salmonids. Pages 52-91 in A. P. Hendry and S. C. Stearns, editors. *Evolution Illuminated: Salmon and Their Relatives*. Oxford University Press, New York.
- Hendry, A. P., and O. K. Berg. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. *Canadian Journal of Zoology* 77:1663-1675.
- Hendry, A. P., and T. Day. 2005. Population structure attributable to reproductive time: isolation by time and adaptation by time. *Molecular Ecology* 14:901-916.
- Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn. 2000. Rapid evolution of reproductive isolation in the wild: Evidence from introduced salmon. *Science* 290:516-518.
- Hess, J. E., A. P. Matala, J. S. Zendt, C. R. Frederiksen, B. Sharp, and S. R. Narum. 2011. Introgressive hybridization among major Columbia River Chinook salmon (*Oncorhynchus tshawytscha*) lineages within the Klickitat River due to hatchery practices. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1876-1891.
- Hess, J. E., and S. R. Narum. 2011. Single-nucleotide polymorphism (SNP) loci correlated with run timing in adult Chinook salmon from the Columbia River basin. *Transactions of the American Fisheries Society* 140:855-864.
- High, B., C. A. Peery, and D. H. Bennett. 2006. Temporary staging of Columbia River summer steelhead in coolwater areas and its effect on migration rates. *Transactions of the American Fisheries Society* 135:519-528.
- Hill, M. F., A. Hastings, and L. W. Botsford. 2002. The effects of small dispersal rates on extinction times in structured metapopulation models. *American Naturalist* 160:389-402.
- Hino, H., T. Iwai, M. Yamashita, and H. Ueda. 2007. Identification of an olfactory imprinting-related gene in the lacustrine sockeye salmon, *Oncorhynchus nerka*. *Aquaculture* 273:200-208.
- Hino, H., N. G. Miles, H. Bando, and H. Ueda. 2009. Molecular biological research on olfactory chemoreception in fishes. *Journal of Fish Biology* 75:945-959.

- Hoar, W. S. 1988. The physiology of smolting salmonids. Pages 275-344 in W. S. Hoar and D. J. Randall, editor. The physiology of developing fish: viviparity and posthatching juveniles. Academic Press. San Diego, CA.
- Hodgson, S., and T. P. Quinn. 2002. The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. Canadian Journal of Zoology-Revue Canadienne De Zoologie 80:542-555.
- Insulander, C., and B. Ragnarsson. 2001. Homing patterns of Baltic salmon, *Salmo salar* L., from smolts released from two hatcheries in the River Dalälven, Sweden. Fisheries Management and Ecology 8:61-67.
- Isaksson, A., S. Oskarsson, S. M. Einarsson, and J. Jonasson. 1997. Atlantic salmon ranching: past problems and future management. ICES Journal of Marine Science 54:1188-1199.
- Johnsen, P. B. 1982. A behavioral control model for homestream selection in migratory salmonids. Pages 266-273 in E. L. Brannon and E. O. Salo, editors. Salmon and trout migratory behavior symposium. University of Washington School of Fisheries. Seattle.
- Johnson, E. L., T. S. Clabough, C. C. Caudill, M. L. Keefer, C. A. Peery, and M. C. Richmond. 2010. Migration depths of adult steelhead (*Oncorhynchus mykiss*) in relation to dissolved gas supersaturation in a regulated river system. Journal of Fish Biology 76:1520-1528.
- Johnson, E. L., T. S. Clabough, D. H. Bennett, T. C. Bjornn, C. A. Peery, C. C. Caudill, and L. C. Stuehrenberg. 2005. Migration depths of adult spring and summer Chinook salmon in the lower Columbia and Snake Rivers in relation to dissolved gas supersaturation. Transactions of the American Fisheries Society 134:1213-1227.
- Johnson, S. L., M. F. Solazzi, and T. E. Nickelson. 1990. Effects on survival and homing of trucking hatchery yearling coho salmon to release sites. North American Journal of Fisheries Management 10:427-433.
- Johnson, R. C., P. K. Weber, J. D. Wikert, M. L. Workman, R. B. MacFarlane, M. J. Grove, and A. K. Schmitt. 2012. Managed metapopulations: do salmon hatchery 'sources' lead to in-river 'sinks' in conservation? PLoS One 7:e28880.
- Johnstone, K. A., K. P. Lubieniecki, B. F. Koop, and W. S. Davidson. 2011. Expression of olfactory receptors in different life stages and life histories of wild Atlantic salmon (*Salmon salar*). Molecular Ecology 20:4059-4069.
- Jonsson, B., N. Jonsson, and L. P. Hansen. 2003. Atlantic salmon straying from the River Imsa. Journal of Fish Biology 62:641-657.
- Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River basin. Science 290:977-979.

- Keefer, M. L., and C. C. Caudill. 2010. A review of adult salmon and steelhead life history and behavior in the Willamette River basin: identification of knowledge gaps and research needs. Technical Report 2010-8 by University of Idaho to U.S. Army Corps of Engineers, Portland, Oregon.
- Keefer, M. L., C. T. Boggs, C. A. Peery, and C. C. Caudill. 2008c. Overwintering distribution, behavior, and survival of adult summer steelhead: variability among Columbia River populations. *North American Journal of Fisheries Management* 28:81-96.
- Keefer, M. L., C. C. Caudill, C. A. Peery, and T. C. Bjornn. 2006a. Route selection in a large river during the homing migration of Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 63:1752-1762.
- Keefer, M. L., C. C. Caudill, C. A. Peery. 2011. Temperature regimes during upstream migration and the use of thermal refugia by adult salmon and steelhead in the Columbia River basin. Letter report to U.S. Army Corps of Engineers.
- Keefer, M. L., C. C. Caudill, C. A. Peery, and S. R. Lee. 2008b. Transporting juvenile salmonids around dams impairs adult migration. *Ecological Applications* 18:1888-1900.
- Keefer, M. L., C. C. Caudill, C. A. Peery, and C. T. Boggs. 2008a. Non-direct homing behaviours by adult Chinook salmon in a large, multi-stock river system. *Journal of Fish Biology* 72:27-44.
- Keefer, M. L., C. A. Peery, and C. C. Caudill. 2006b. Long-distance downstream movements by homing adult Chinook salmon (*Oncorhynchus tshawytscha*). *Journal of Fish Biology* 68:944-950.
- Keefer, M. L., C. A. Peery, and M. J. Heinrich. 2008e. Temperature-mediated en route migration mortality and travel rates of endangered Snake River sockeye salmon. *Ecology of Freshwater Fish* 17:136-145.
- Keefer, M. L., C. A. Peery, and B. High. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1734-1747.
- Keefer, M. L., R. H. Wertheimer, A. F. Evans, C. T. Boggs, and C. A. Peery. 2008d. Iteroparity in Columbia River summer-run steelhead (*Oncorhynchus mykiss*): implications for conservation. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2592-2605.
- Keefer, M. L., C. A. Peery, J. Firehammer, and M. L. Moser. 2005. Straying rates of known-origin adult Chinook salmon and steelhead within the Columbia River basin, 2000-2003. Technical Report 2005-5 of Idaho Cooperative Fish and Wildlife Research Unit.

- Kelsey, D. A., C. B. Schreck, J. L. Congleton, and L. E. Davis. 2002. Effects of juvenile steelhead on juvenile Chinook salmon behavior and physiology. *Transactions of the American Fisheries Society* 131:676-689.
- Kenaston, K. R., R. B. Lindsay, and R. K. Schroeder. 2001. Effect of acclimation on the homing and survival of hatchery winter steelhead. *North American Journal of Fisheries Management* 21:765-773.
- Klaprat, D. A., R. E. Evans, and T. J. Hara. 1992. Environmental contaminants and chemoreception in fishes. Pages 321-341 *in* T. J. Hara, editor. *Fish chemoreception*. Chapman and Hall. New York.
- Kostow, K. E., A. R. Marshall, and S. R. Phelps. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. *Transactions of the American Fisheries Society* 132:780-790.
- Kostow, K. E., and S. Zhou. 2006. The effect of an introduced summer steelhead hatchery stock on the productivity of a wild winter steelhead population. *Transactions of the American Fisheries Society* 135:825-841.
- Labelle, M. 1992. Straying patterns of coho salmon (*Oncorhynchus kisutch*) stocks from southeastern Vancouver Island, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1843-1855.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* 142:911-927.
- Leggett, W. C. 1977. The ecology of fish migrations. *Annual Review of Ecology and Systematics* 8:285-308.
- Leider, S. A. 1989. Increased straying by adult steelhead trout, *Salmo gairdneri*, following the 1980 eruption of Mount St. Helens. *Environmental Biology of Fishes* 24:219-229.
- Lema, S. C., and G. A. Nevitt. 2004. Evidence that thyroid hormone induces olfactory cellular proliferation in salmon during a sensitive period for imprinting. *Journal of Experimental Biology* 207:3317-3327.
- LePage, C., and P. Cury. 1997. Population viability and spatial fish reproductive strategies in constant and changing environments: an individual-based modeling approach. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2235-2246.
- Levin, P. S., R. W. Zabel, and J. G. Williams. 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268:1153-1158.

- Lin, J. E., R. Hilborn, T. P. Quinn, and L. Hauser. 2011. Self-sustaining populations, population sinks or aggregates of strays: chum (*Oncorhynchus keta*) and Chinook salmon (*Oncorhynchus tshawytscha*) in the Wood River system, Alaska. *Molecular Ecology* 20:4925-4937.
- Lin, J., T. P. Quinn, R. Hilborn, and L. Hauser. 2008. Fine-scale differentiation between sockeye salmon ecotypes and the effect of phenotype on straying. *Heredity* 101:341-350.
- Lirette, M. G., and R. S. Hooton. 1988. Coded-wire tag recoveries from Vancouver Island sport caught steelhead 1982-1986. Fisheries Management Report 92, Nanaimo, British Columbia.
- Marchetti, M. P., and G. A. Nevitt. 2003. Effects of hatchery rearing on brain structures of rainbow trout, *Oncorhynchus mykiss*. *Environmental Biology of Fishes* 66:9-14.
- Marsh, D. M., W. D. Muir, B. P. Sandford, S. G. Smith, and D. Elliott. 2012. Alternative barging strategies to improve survival of salmonids transported from Lower Granite Dam: Final report from the 2006-2008 spring/summer Chinook salmon and steelhead juvenile migrations. National Marine Fisheries Service, Seattle, Washington.
- Matala, A. P., S. R. Narum, W. Young, and J. L. Vogel. 2012. Influences of hatchery supplementation, spawner distribution, and habitat on genetic structure of Chinook salmon in the South Fork Salmon River, Idaho. *North American Journal of Fisheries Management* 32:346-359.
- Maule, A. G., C. B. Schreck, C. S. Bradford, and B. A. Barton. 1988. Physiological effects of collecting and transporting emigrating juvenile Chinook salmon past dams on the Columbia River. *Transactions of the American Fisheries Society* 117:245-261.
- Mayer, K., M. Schuck, and P. Iversen. 2010. Assess salmonids in the Asotin Creek watershed, 2009 Annual Report. Report by Washington Department of Fish and Wildlife for Bonneville Power Administration. BPA Project # 2002-053-00.
- McCabe, G. T., C. W. Long, and S. L. Leek. 1983. Survival and homing of juvenile coho salmon, *Oncorhynchus kisutch*, transported by barge. *Fisheries Bulletin* 81:412-415.
- McClure, M. M., E. E. Holmes, B. L. Sanderson, and C. E. Jordan. 2003. A large-scale, multispecies status, assessment: Anadromous salmonids in the Columbia River Basin. *Ecological Applications* 13:964-989.
- McCormick, S. D. 2009. Evolution of the hormonal control of animal performance: insights from the seaward migration of salmon. *Integrative and Comparative Biology* 49:408-422.
- McCormick, S. D., L. P. Hansen, T. P. Quinn, and R. L. Saunders. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 55(Suppl. 1):77-92.

- McCormick, S. D., M. F. O'Dea, A. M. Moeckel, and B. T. Bjornsson. 2003. Endocrine and physiological changes in Atlantic salmon smolts following hatchery release. *Aquaculture* 222:45-57.
- McCormick, S. D., R. L. Saunders, E. B. Henderson, and P. R. Harmon. 1987. Photoperiod control of parr-smolt transformation in Atlantic salmon (*Salmo salar*): changes in salinity tolerance, gill Na^+ , K^+ -ATPase activity, and plasma thyroid hormones. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1462-1468.
- McDowall, R. M. 1990. *New Zealand freshwater fishes: a natural history and guide*. Heinmann-Reed. Auckland, New Zealand.
- McDowall, R. M. 2001. Anadromy and homing: two life-history traits with adaptive synergies in salmonid fishes? *Fish and Fisheries* 2:78-85.
- McGinnity, P., P. Prodöhl, A. Ferguson, R. Hynes, N. ÓMaoiléidigh, N. Baker, D. Cotter, B. O'Hea, D. Cooke, G. Rogan, J. Taggart, and T. Cross. 2003 special spellings. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270:2443-2450.
- McGinnity, P., C. Stone, J. B. Taggart, D. Cooke, D. Cotter, R. Hynes, C. McCamley, T. Cross, and A. Ferguson. 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES Journal of Marine Science* 54:998-1008.
- McIsaac, D. O., and T. P. Quinn. 1988. Evidence for a hereditary component in homing behavior of Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 45:2201-2205.
- McLean, J. E., P. Bentzen, and T. P. Quinn. 2003. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead trout (*Oncorhynchus mykiss*) through the adult stage. *Canadian Journal of Fisheries and Aquatic Sciences* 60:433-440.
- Mendel, G., and M. Schuck. 1989. Migration patterns of Wallowa stock hatchery steelhead in the Snake and Grande Ronde rivers of Washington. Report #AFF1/LSR-89-03 of Washington Department of Wildlife, Dayton, WA.
- Milks, D., M. Varney, and M. Schuck. 2006. Lyons Ferry Hatchery Evaluation fall Chinook salmon annual report: 2006. Washington Department of Fish and Wildlife, Olympia, Washington.
- Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1994. Exotic species and the integrity of the Great Lakes. *Bioscience* 44(10):666-676.

- Milner, A. M., and R. G. Bailey. 1989. Salmonid colonization of new streams in Glacier Bay National Park, Alaska. *Aquaculture and Fisheries Management* 20:179-192.
- Moore, A., N. Lower, I. Mayer, and L. Greenwood. 2007. The impact of a pesticide on migratory activity and olfactory function in Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture* 273:350-359.
- Moore, A., and A. P. Scott. 1991. Testosterone is a potent odorant in precocious male Atlantic salmon (*Salmon salar* L.) parr. *Philosophical transactions of the Royal Society B* 332:241-244.
- Morbey, Y. E., C. E. Brassil, and A. P. Hendry. 2005. Rapid senescence in Pacific salmon. *The American Naturalist* 166:556-568.
- Moore, A., and N. Lower. 2001. The impact of two pesticides on olfactory-mediated endocrine function in mature male Atlantic salmon (*Salmo salar* L.) parr. *Comparative Biochemistry and Physiology Part B* 129:269-276.
- Morin, P. -P., O. Andersen, E. Haug, and K. B. Doving. 1994. Changes in serum-free thyroxine, prolactin, and olfactory activity during induced smoltification in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 51:1985-1992.
- Morin, P.-P., J. J. Dodson, and F. Y. Doré. 1989. Thyroid activity concomitant with olfactory learning and heart rate changes in Atlantic salmon, *Salmo salar*, during smoltification. *Canadian Journal of Fisheries and Aquatic Sciences* 46:131-136.
- Morin, P. -P., and K. B. Døving. 1992. Changes in the olfactory function of Atlantic salmon, *Salmo salar*, in the course of smoltification. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1704-1713.
- Mortensen, D. G., A. C. Wertheimer, J. M. Maselko, and S. G. Taylor. 2002. Survival and straying of Auke Creek, Alaska, pink salmon marked with coded wire tags and thermally induced otolith marks. *Transactions of the American Fisheries Society* 131:14-26.
- Muir, W. D., D. M. Marsh, B. J. Sandford, S. G. Smith, and J. G. Williams. 2006. Post-hydropower system delayed mortality of transported Snake River stream-type Chinook salmon: unraveling the mystery. *Transactions of the American Fisheries Society* 135:1523-1534.
- Murdoch, A. R., M. A. Tonseth, and T. L. Miller. 2009. Migration patterns and spawning distribution of adult hatchery sockeye salmon released as parr from net-pens in Lake Wenatchee, Washington. *North American Journal of Fisheries Management* 29:447-459.
- Narum, S. R., S. Boe, P. Moran, and M. Powell. 2006a. Small-scale genetic structure and variation in steelhead of the Grande Ronde River, Oregon, USA. *Transactions of the American Fisheries Society* 135:979-986.

- Narum, S. R., M. S. Powell, R. Evenson, B. Sharp, and A. J. Talbot. 2006b. Microsatellites reveal population substructure of Klickitat River native steelhead and genetic divergence from an introduced stock. *North American Journal of Fisheries Management* 26:147-155.
- Narum, S. R., T. L. Schultz, D. M. Van Doornik, and D. Teel. 2008. Localized genetic structure persists in wild populations of Chinook salmon in the John Day River despite gene flow from outside sources. *Transactions of the American Fisheries Society* 137:1650-1656.
- Narum, S. R., J. J. Stephenson, and M. R. Campbell. 2007. Genetic variation and structure of Chinook salmon life history types in the Snake River. *Transactions of the American Fisheries Society* 136:1252-1262.
- Naughton, G. P., C. C. Caudill, M. L. Keefer, T. C. Bjornn, L. C. Stuehrenberg, and C. A. Peery. 2005. Late-season mortality during migration of radio-tagged sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* 62:30-47.
- Naughton, G. P., M. A. Jepson, C. A. Peery, C. V. Brun, and J. C. Graham. 2009. Effects of temporary tributary use on escapement estimates of adult fall Chinook salmon in the Deschutes River, Oregon. *North American Journal of Fisheries Management* 29:1511-1518.
- Neave, F. 1964. Ocean migrations of Pacific salmon. *Journal of the Fisheries Research Board of Canada* 21:1227-1244.
- Neville, H. M., D. J. Isaak, J. B. Dunham, R. F. Thurow, and B. E. Rieman. 2006. Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: insights from spatial autocorrelation analysis of individual genotypes. *Molecular Ecology* 15:4589-4602.
- Nevitt, G., and A. Dittman. 1999. A new model for olfactory imprinting in salmon. *Integrative Biology* 1:215-223.
- Nevitt, G. A., A. H. Dittman, T. P. Quinn, and J. W.J. Moody. 1994. Evidence for a peripheral olfactory memory in imprinted salmon. *Proceedings of the National Academy of Sciences of the United States of America* 91:4288-4292.
- Nevitt, G. A., and S. Lema. 2002. Testing a new model for olfactory imprinting in salmon: evidence for proliferation of olfactory receptor neurons in response to thyroid hormone. *Integrative and Comparative Biology* 42:1284-1285.
- Nishioka, R. S., G. Young, H. A. Bern, W. Jochimsen, and C. Hiser. 1985. Attempts to intensify the thyroxin surge in coho and king salmon by chemical stimulation. *Aquaculture* 45:215-225.

- Nordeng, H. 1971. Is the local orientation of anadromous fishes determined by pheromones? *Nature* 233:411-413.
- Nordeng, H. 1977. A pheromone hypothesis for homeward migration in anadromous salmonids. *Oikos* 28:155-159.
- Nordeng, H. 2008. Char ecology: natal homing in sympatric populations of anadromous Arctic char *Salvelinus alpinus* (L.): roles of pheromone recognition. *Ecology of Freshwater Fish* 48:41-51.
- Økland, F., J. Erkinaro, K. Moen, E. Niemelä, P. Fiske, R. S. McKinley, and E. B. Thorstad. 2001. Return migration of Atlantic salmon in the River Tana: phases of migratory behavior. *Journal of Fish Biology* 59:862-874.
- Olsen, J. B., T. D. Beacham, M. Wetklo, L. W. Seeb, C. T. Smith, B. G. Flannery, and J. K. Wenburg. 2010. The influence of hydrology and waterway distance on population structure of Chinook salmon *Oncorhynchus tshawytscha* in a large river. *Journal of Fish Biology* 76:1128-1148.
- Olson, A. F., and T. P. Quinn. 1993. Vertical and horizontal movements of adult Chinook salmon *Oncorhynchus tshawytscha* in the Columbia River estuary. *Fishery Bulletin* 91:171-178.
- Pascual, M. A., and T. P. Quinn. 1994. Geographical patterns of straying of fall Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), from Columbia River (USA) hatcheries. *Aquaculture and Fisheries Management* 25(S2):17-30.
- Pascual, M. A., T. P. Quinn, and H. Fuss. 1995. Factors affecting the homing of fall Chinook salmon from Columbia River hatcheries. *Transactions of the American Fisheries Society* 124:308-320.
- Peacock, S. J., and C. A. Holt. 2012. Metrics and sampling designs for detecting trends in the distribution of spawning Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 69:681-694.
- Perrier, C., G. Evanno, J. Belliard, R. Guyomard, and J.-L. Baglinière. 2010. Natural recolonization of the Seine River by Atlantic salmon (*Salmo salar*) of multiple origins. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1-4.
- Pess, G. R. 2009. Patterns and processes of salmon colonization. Ph.D. thesis. Aquatic and Fishery Sciences, University of Washington.
- Pess, G. R., R. Hilborn, K. Kloehn, and T. P. Quinn. 2012. The influence of population dynamics and environmental conditions on pink salmon (*Oncorhynchus gorbuscha*) recolonization after barrier removal in the Fraser River, British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 69:970-982.

- Peterson, N. P. 1982. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1308-1310.
- Power, D. M., L. Llewellyn, M. Faustino, M. A. Nowell, B. T. Bjornsson, I. E. Einarsdottir, A. V. M. Canario, and G. E. Sweeney. 2001. Thyroid hormones in growth and development of fish. *Comparative Biochemistry and Physiology Part C* 130:447-459.
- Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. American Fisheries Society. Bethesda, Maryland.
- Quinn, T. P. 1984. Homing and straying in Pacific salmon. Pages 357-362 in J. D. McLeavey, G. P. Arnold, J. J. Dodson and W. H. Neill, editors. *Mechanisms of migration in fishes*. Plenum Press. New York.
- Quinn, T. P. 1990. Current controversies in the study of salmon homing. *Ethology Ecology and Evolution* 2:49-63.
- Quinn, T. P. 1993. A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research* 18:29-44.
- Quinn, T. P., E. L. Brannon, and A. H. Dittman. 1989a. Spatial aspects of imprinting and homing in coho salmon, *Oncorhynchus kisutch*. *Fisheries Bulletin* 87:769-774.
- Quinn, T. P., and K. Fresh. 1984. Homing and straying in Chinook salmon (*Oncorhynchus tshawytscha*) from Cowlitz River Hatchery, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1078-1082.
- Quinn, T. P., M. T. Kinnison, and M. J. Unwin. 2001. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* 112:493-513.
- Quinn, T. P., R. S. Nemeth, and D. O. McIsaac. 1991. Homing and straying patterns of fall Chinook salmon in the lower Columbia River. *Transactions of the American Fisheries Society* 120:150-156.
- Quinn, T. P., J. H. B. Rich, D. Gosse, and N. Schtickzelle. 2012. Population dynamics and asynchrony at fine spatial scales: a case history of sockeye salmon (*Oncorhynchus nerka*) population structure in Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 69:297-306.
- Quinn, T. P., I. J. Stewart, and C. P. Boatright. 2006. Experimental evidence of homing to site of incubation by mature sockeye salmon, *Oncorhynchus nerka*. *Animal Behaviour* 72:941-949.
- Quinn, T. P., and R. F. Tallman. 1987. Seasonal environmental predictability and homing in riverine fishes. *Environmental Biology of Fishes* 18:155-159.

- Quinn, T. P., B. A. Terhart, and C. Groot. 1989b. Migratory orientation and vertical movements of homing adult sockeye salmon, *Oncorhynchus nerka*, in coastal waters. *Animal Behaviour* 37:587-599.
- Quinn, T. P., and G. M. Tolson. 1986. Evidence of chemically mediated population recognition in coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Zoology* 64:84-87.
- Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2011. Contemporary divergence in migratory timing of naturalized populations of Chinook salmon *Oncorhynchus tshawytscha*, in New Zealand. *Evolutionary Ecology Research* 13:45-54.
- Quinn, T. P., E. C. Volk, and A. P. Hendry. 1999. Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology* 77:766-775.
- Reisenbichler, R. R. 1988. Relation between distance transferred from natal stream and recovery rate for hatchery coho salmon. *North American Journal of Fisheries Management* 8:172-174.
- Reisenbichler, R. R., and S. P. Rubin. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. *ICES Journal of Marine Science* 56:459-466.
- Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 27-160 in R. C. Simon and P. A. Larkin, editors. *The stock concept in Pacific salmon*. University of British Columbia, Vancouver, British Columbia.
- Riddell, B. E., and W. C. Leggett. 1981. Evidence of an adaptive basis for geographic variation of body morphology, and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 38:308-320.
- Ruzycki, J. R., and R. W. Carmichael. 2010. Preliminary summary of out-of-basin strays in the John Day River basin. Oregon Department of Fish and Wildlife, La Grande, Oregon.
- Schaller, H., P. Wilson, S. Haeseker, C. Petrosky, E. Tinus, T. Dalton, R. Woodin, E. Weber, N. Bouwes, T. Berggren, J. McCann, S. Rassk, H. Franzoni, and P. McHugh. 2007. Comparative survival study (CSS) of PIT-tagged spring/summer Chinook and summer steelhead: ten-year retrospective analyses report. BPA Contract #19960200 and #00025634. 377 pp.
- Scholz, A. T., R. M. Horrall, J. C. Cooper, and A. D. Hasler. 1976. Imprinting to chemical cues: the basis for home stream selection in salmon. *Science* 192:1247-1249.
- Scholz, N. L., N. K. Truelove, B. L. French, B. A. Berejikian, T. P. Quinn, E. Casillas, and T. K. Collier. 2000. Diazinon disrupts antipredator and homing behaviors in Chinook salmon

- (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 57:1911-1918.
- Schroeder, R. K., K. R. Kenaston, and L.K. Mclaughlin. 2007. Progress reports 2006-2007: spring Chinook salmon in the Willamette and Sandy river. Oregon Department of Fish and Wildlife, Salem, Oregon.
- Schroeder, R. K., R. B. Lindsay, and K. R. Kenaston. 2001. Origin and straying of hatchery winter steelhead in Oregon coastal rivers. Transactions of the American Fisheries Society 130:431-441.
- Schtickzelle, N., and T. P. Quinn. 2007. A metapopulation perspective for salmon and other anadromous fish. Fish and Fisheries 8:297-314.
- Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game, Fish Bulletin 98:1-375.
- Sharp, D., S. Sharr, and C. Peckham. 1994. Homing and straying patterns of coded wired tagged pink salmon in Prince William Sound. Pages 77-82 Proceedings of the 16th Northeast Pacific pink and chum salmon workshop. Alaska Sea Grant College Program, Juneau, Alaska.
- Sholes, W. H., and R. J. Hallock. 1979. An evaluation of rearing fall-run Chinook salmon, *Oncorhynchus tshawytscha*, to yearlings at Feather River Hatchery, with a comparison of returns from hatchery and downstream releases. California Department of Fish and Game 65:239-255.
- Shrimpton, J. M., N. J. Bernier, and D. J. Randall. 1994. Changes in cortisol dynamics in wild and hatchery-reared juvenile coho salmon (*Oncorhynchus kisutch*) during smoltification. Canadian Journal of Fisheries and Aquatic Sciences 51:2179-2187.
- Slaney, P. A., L. Berg, and A. F. Tautz. 1993. Returns of hatchery steelhead relative to site of release below an upper-river hatchery. North American Journal of Fisheries Management 13:558-566.
- Slatick, E., L. G. Gilbreath, J. R. Harmon, T. C. Bjornn, R. R. Ringe, K. A. Walch, A. J. Novotny, and W. S. Zaugg. 1981. Imprinting hatchery reared salmon and steelhead trout for homing, 1978-1983. Report of National Oceanic and Atmospheric Administration to Bonneville Power Administration, Seattle, Washington.
- Slatick, E., D. L. Park, and W. J. Ebel. 1975. Further studies regarding effects of transportation on survival and homing of Snake River Chinook salmon and steelhead trout. Fishery Bulletin 73:925-931.

- Solazzi, M. F., T. E. Nickelson, and S. L. Johnson. 1991. Survival, contribution, and return of hatchery coho salmon (*Oncorhynchus kisutch*) released into freshwater, estuarine, and marine environments. *Canadian Journal of Fisheries and Aquatic Sciences* 48:248-253.
- Solomon, D. J. 1973. Evidence for pheromone-influenced homing by migrating Atlantic salmon, *Salmo salar*. *Nature* 244:231-232.
- Stephenson, S. A. 2006. A review of the occurrence of Pacific salmon (*Oncorhynchus* spp.) in the Canadian Western Arctic. *Arctic* 59:37-46.
- Stewart, I. J., T. P. Quinn, and P. Bentzen. 2003. Evidence for fine-scale natal homing among island beach spawning sockeye salmon, *Oncorhynchus nerka*. *Environmental Biology of Fishes* 67:77-85.
- Sundell, K., C. Dellefors, and B. T. Bjørnsson. 1998. Wild and hatchery-reared brown trout, *Salmon trutta*, differ in smolt related characteristics during parr-smolt transformation. *Aquaculture* 167:53-65.
- Tallman, R. F and M. C. Healey. 1994. Homing, straying, and gene flow among seasonally separated populations of chum salmon (*Oncorhynchus keta*). *Canadian Journal of Fisheries and Aquatic Sciences* 51:577-588.
- Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98:185-207.
- Tessier, N., and L. Bernatchez. 1999. Stability of population structure and genetic diversity across generations assessed by micro-satellites among sympatric populations of landlocked Atlantic salmon (*Salmo salar* L.). *Molecular Ecology* 8:169-179.
- Thedinga, J. F., A. C. Wertheimer, R. A. Heintz, J. M. Maselko, and S. D. Rice. 2000. Effects of stock, coded-wire tagging, and transplant on straying of pink salmon in southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 57:2076-2085.
- Thorpe, J. E. 1994. Salmonid flexibility: responses to environmental extremes. *Transactions of the American Fisheries Society* 123:606-612.
- Thorstad, E. B., T. G. Heggberget, and F. Økland. 1998. Migratory behaviour of adult wild and escaped farmed Atlantic salmon, *Salmo salar* L., before, during and after spawning in a Norwegian river. *Aquaculture Research* 29:419-428.
- Tierney, K. B., D. H. Baldwin, T. J. Hara, P. S. Ross, N. L. Scholz, and C. J. Kennedy. 2010. Olfactory toxicity in fishes. *Aquatic Toxicology* 90:2-26.
- Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of Chinook salmon in northeastern Oregon. *Ecological Applications* 9:301-319.

- Tuomikoski, J., J. McCann, T. Berggren, H. Schaller, P. Wilson, S. Haeseker, J. Fryer, C. Petrosky, E. Tinus, T. Dalton, and R. Ehlke. 2010. Comparative survival study (CSS) of PIT-tagged spring/summer Chinook and summer steelhead. 2010 Annual Report. BPA Contract #19960200. 186 pp.
- Tuomikoski, J., J. McCann, T. Berggren, H. Schaller, P. Wilson, S. Haeseker, J. Fryer, C. Petrosky, E. Tinus, T. Dalton, and R. Ehlke. 2011. Comparative survival study (CSS) of PIT-tagged spring/summer Chinook and summer steelhead. 2011 Annual Report. BPA Contract #19960200. 186 pp.
- Ueda, H. 2011. Physiological mechanism of homing migration in Pacific salmon from behavioral to molecular to biological approaches. *General and Comparative Endocrinology* 170:222-232.
- Ueda, H. 2012. Physiological mechanisms of imprinting and homing migration in Pacific salmon *Oncorhynchus* spp. *Journal of Fish Biology*
- Ueda, K., T. J. Hara, and A. Gorbman. 1967. Electroencephalographic studies on olfactory discrimination in adult spawning salmon. *Comparative Biochemistry and Physiology* 21:133-143.
- Ueda, H., and K. Yamauchi. 1995. Biochemistry of fish migration. Pages 265-279 in P. W. Hochachka and T. P. Mommsen, editors. *Biochemistry and molecular biology of fishes*, Volume 5. Elsevier. Amsterdam.
- Unwin, M. J., and T. P. Quinn. 1993. Homing and straying patterns of Chinook salmon (*Oncorhynchus tshawytscha*) from a New Zealand hatchery: Spatial distribution of strays and effects of release date. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1168-1175.
- Utter, F. 1998. Genetic problems of hatchery-reared progeny released into the wild, and how to deal with them. *Bulletin of Marine Science* 62:623-640.
- Vasemägi, A., R. Gross, T. Paaver, M.-L. Kojonen, and J. Nilsson. 2005. Extensive immigration from compensatory hatchery releases into wild Atlantic salmon population in the Baltic Sea: spatio-temporal analysis over 18 years. *Heredity* 95:76-83.
- Virtanen, E., and A. Soivio. 1985. The patterns of T3, T4, cortisol and Na⁺K⁺ -ATPase during smoltification of hatchery-reared *Salmon salar* and comparison with wild smolts. *Aquaculture* 45:97-109. (abstract only)
- Volpe, J. P., E. B. Taylor, D. W. Rimmer, and B. W. Glickman. 2000. Evidence of natural reproduction of aquaculture-escaped Atlantic salmon in a coastal British Columbia river. *Conservation Biology* 14:899-903.

- Vreeland, R. R., R. J. Wahle, and A. H. Arp. 1975. Homing behavior and contribution to Columbia River fisheries of marked coho salmon released at two locations. *Fisheries Bulletin* 73:717-725.
- Wagner, H. H. 1969. Effect of stocking location of juvenile steelhead trout, *Salmo gairdneri*, on adult catch. *Transactions of the American Fisheries Society* 98:27-34.
- Walter, R. P., T. Aykanat, D. W. Kelly, J. M. Shrimpton, and D. D. Heath. 2009. Gene flow increases temporal stability of Chinook salmon (*Oncorhynchus tshawytscha*) populations in the Upper Fraser River, British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 66:167-176.
- Waples, R. S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* 48(supp 1):124-133.
- Waples, R. S., R. G. Gustafson, L. A. Weitkamp, J. M. Myers, O. W. Johnson, P. J. Busby, J. J. Hard, G. J. Bryant, F. W. Waknitz, K. Neely, D. Teel, W. S. Grant, G. A. Winans, S. Phelps, A. Marshall, and B. M. Baker. 2001. Characterizing diversity in salmon from the Pacific Northwest. *Journal of Fish Biology* 59:1-41.
- Waples, R. S., G. R. Pess, and T. Beechie. 2008. Evolutionary history of Pacific salmon in dynamic environments. *Evolutionary Applications* 1:189-206.
- Waples, R. S., D. J. Teel, J. M. Meyer, and A. R. Marshall. 2004. Life-history divergence in Chinook salmon: historic contingency and parallel evolution. *Evolution* 58:386-403.
- Ward, D. L., R. R. Boyce, F. R. Young, and F. E. Olney. 1997. A review and assessment of transportation studies for juvenile Chinook salmon in the Snake River. *North American Journal of Fisheries Management* 17:652-662.
- Weissburg, M. J. 2000. The fluid dynamical context of chemosensory behavior. *Biological Bulletin* 198:188-202.
- Welker, T. L., and J. L. Congleton. 2009. Preliminary examination of oxidative stress in juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*) of wild origin sampled from transport barges. *Journal of Fish Biology* 75:1895-1905.
- Wertheimer, A. C., R. A. Heintz, J. F. Thedinga, J. M. Maselko, and S. D. Rice. 2000. Straying of adult pink salmon from their natal stream following embryonic exposure to weathered *Exxon Valdez* crude oil. *Transactions of the American Fisheries Society* 129:989-1004.
- Westerberg, H. 1982. The orientation of fish and their vertical stratification at fine- and micro-scales. Pages 179-203 in J. D. McCleave, G. P. Arnold, J. J. Dodson and W. H. Neill, editors. *Mechanisms of migration in fishes*. Plenum Press, New York.

- Williamson, K. S., A. R. Murdoch, T. N. Pearsons, E. J. Ward, and M. J. Ford. 2010. Factors influencing the relative fitness of hatchery and wild spring Chiook salmon (*Oncorhynchus tshawytscha*) in the Wenatchee River, Washington, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1840-1851.
- Wisby, W. J., and A. D. Hasler. 1954. Effect of olfactory occlusion on migrating silver salmon (*O. kisutch*). *Journal of the Fisheries Research Board of Canada* 11:472-478.
- Withler, F. C. 1982. Transplanting Pacific salmon. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1079:1-27.
- Yamamoto, Y., H. Hino, and H. Ueda. 2010. Olfactory imprinting of amino acids in lacustrine sockeye salmon. *PLoS One* 5:e8633.
- Zaugg, W. S., and H. H. Wagner. 1973. Gill ATPase activity related to parr-smolt transformation and migration in steelhead trout (*Salmon gairdneri*) - influence of photoperiod and temperature. *Comparative Biochemistry and Physiology Part B* 45:955-965.
- Zhivotovsky, L. A., L. K. Fedorova, G. A. Rubtsova, M. V. Shitova, T. A. Rakitskaya, V. D. Prokhorovskaya, B. P. Smirnov, A. M. Kaev, V. M. Chupakhin, V. G. Samarksy, V. P. Pogodin, S. I. Borzov, and K. I. Afanasiev. 2012. Rapid expansion of an enhanced stock of chum salmon and its impacts on wild population components. *Environmental Biology of Fishes* 94(S11):249-258.
- Zimmer-Faust, R. K., C. M. Finelli, N. D. Pentcheff, and D. S. Wetthey. 1995. Odor plumes and animal navigation in turbulent water flow: a field study. *Biological Bulletin* 188:111-116.