

# Homing and straying by anadromous salmonids: a review of mechanisms and rates

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**Abstract** There is a long research history addressing olfactory imprinting, natal homing, and non-natal straying by anadromous salmon and trout (Salmonidae). In undisturbed populations, adult straying is a fundamental component of metapopulation biology, facilitating genetic resilience, demographic stability, recolonization, and range expansion into unexploited habitats. Unfortunately, salmonid hatcheries and other human actions worldwide have affected straying in ways that can negatively affect wild populations through competitive interactions, reduced productivity and resiliency, hybridization and domestication effects, and outbreeding depression. Reduced adult straying is therefore an objective for many managed populations. Currently, there is considerable uncertainty about the range of ‘natural’ stray rates and about which mechanisms precipitate straying in either wild or human-influenced fish. Research in several disciplines indicates that adult straying is affected by endocrine physiology and neurological processes in juveniles, incomplete or interrupted imprinting during rearing and emigration, and by complex interactions among adult maturation processes, reproductive behaviors, olfactory memory, environmental conditions during migration, and senescence physiology.

Reported salmonid stray rates indicate that the behavior varies among species, among life-history types, and among populations within species. Most strays enter sites near natal areas, but long-distance straying also occurs, especially in hatchery populations that were outplanted or transported as juveniles. A majority of past studies has estimated straying as demographic losses *from* donor populations, but some have estimated straying *into* recipient populations. Most recipient-based estimates have substantiated concerns that wild populations are vulnerable to swamping by abundant hatchery and farm-raised strays.

**Keywords** Imprinting · Olfaction · *Oncorhynchus* · Orientation · Philopatry · *Salmo*

## Introduction

Our understanding of homing and straying by anadromous salmonids (*Oncorhynchus*, *Salmo*, and *Salvelinus* species) has primarily been derived from studies of fish physiology and behavior under the purview of hatchery management. Far less is known about wild populations and there is considerable disagreement about the rates of “natural” versus management-related straying. Our objectives in this review are to: (1) consider adult salmonid homing and straying within broad evolutionary, ecological, and management contexts; (2) summarize the mechanisms

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associated with homing versus straying; (3) provide recommendations on a lexicon for the variety of straying behaviors that have been described in the literature; (4) assess potential predictors of straying in wild and human-influenced populations; and (5) synthesize reported straying rates and behaviors across species, life history types, and populations.

### Evolutionary context

Philopatry (i.e., homing) to natal sites is a fundamental life-history trait of most anadromous salmon and trout. 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 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, and ranges 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 typically defined as adult migration to—and attempted reproduction at—non-natal sites (Quinn 1993). In the context of hatcheries and other human interventions, straying is often negatively framed as a “failure to home”. However, straying in wild populations is a critical evolutionary feature of salmonid biology that compliments homing. Straying can be adaptive over short ecological time frames and at longer evolutionary scales. It is therefore useful to distinguish proximate factors that affect straying, such as sensory ecology and the physiology of orientation and reproduction, from the ultimate factors that have led to the evolution and maintenance of straying. Both contribute to the observed variability in straying among populations and understanding these effects is necessary to interpret behaviors and set management goals (e.g., if managing for zero straying is not possible, what are “natural” straying rates?).

It is clear that straying buffers against spatial and temporal variation in habitat quality, and allows colonization of new habitats (Milner and Bailey 1989; Burger et al. 1997; Quinn et al. 2001; Stephenson 2006)

and recolonization after local extinction (Withler 1982; Anderson and Quinn 2007; Perrier et al. 2010; Pess et al. 2012). Straying also reduces inbreeding depression and density dependent effects such as competition among related individuals (Quinn 1993; Hendry et al. 2004). It is less clear whether some individuals 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 disperse in the face of temporary or catastrophic environmental fluctuations. Indeed, salmonids are increasingly considered in terms of metapopulations connected by some degree of movement (i.e., straying) among populations.

### 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 areas 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 hold in suitable habitat for weeks to months prior to the onset of spawning; this 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.

The relative ecological stability and quality of spawning and rearing habitats can be a good predictor of homing rates. 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; 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. 2013).

Straying is just one component of salmonid life history that varies within and among populations in response to habitat stability. 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. Phenotypic plasticity during juvenile stages (e.g., in behavior or physiology) can maximize survival to adulthood given the availability and predictability of suitable habitats. In comparison, plasticity in adult life history temporally spreads the risk of reproductive failure across years (i.e., multiple maturation ages or spawning attempts) or can spread the risk spatially (i.e., by straying to productive sites) (LePage and Cury 1997; Quinn 2005). Importantly, the potential 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, or when there are spatial or temporal mismatches between strays and local spawners that prevent breeding.

The proximate factors that make non-natal habitats attractive to strays have not been conclusively identified in the 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; Hasler and Scholz 1983; 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 exploit locations 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). This pattern 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 a similar ecological setting, including underlying geology, river morphology, and water quality parameters. Water chemistry may be of

particular importance given the use of olfaction for route finding and home site recognition.

#### Fisheries management context

Demographically, straying fish affect two populations: their origin population (i.e., the donor population) and their selected breeding population (i.e., the recipient population). While straying is typically considered as a per capita probability (e.g., 3 %), it is important to consider the absolute number of strays, emigration rates from donor populations, and immigration rates into recipient populations. 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 percentage of returning adults has relatively limited negative effects on the donor population because salmonids have high fecundity and population growth rates are resilient to high levels of adult mortality or reduced homing (Ricker 1972; McClure et al. 2003).

Strays are a demographic gain for recipient populations if they contribute to reproduction or contribute to management-related escapement or harvest objectives. A small number of strays typically 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 overall resilience and genetic stability (Araki et al. 2007; Walter et al. 2009).

Strays have more substantive effects when either the donor or recipient population is small. Small populations can be vulnerable to demographic stochasticity, wherein random or episodic adult mortality, reproductive failure, or skewed sex ratios 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.

The size of the recipient population relative to the donor population is also critically important to

understanding potential effects—both positive and negative—of straying. Straying into a small recipient population potentially contributes to recipient population growth and to its fitness and viability. Indeed, this is a fundamental aspect of salmonid evolution and metapopulation dynamics (Hill et al. 2002; Hendry et al. 2004; 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 successfully breed with the recipient population may dilute locally-adapted traits through introgression. Even low ( $\sim 1\%$ ) rates of straying from large donor populations can numerically swamp small recipient populations. 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 population becomes 500 local fish plus 500 strays (i.e., 50% strays). If the strays have lower fitness in this scenario, the risk of outbreeding depression in the recipient population can be high.

Straying hatchery fish, in particular, have a variety of well-documented negative genetic, ecological, and fitness impacts on wild recipient populations. In addition to outbreeding depression, these include competitive interactions, displacement, reduced productivity, reduced resiliency, plus hybridization and domestication effects (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 anadromous salmonid-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; Utter 1998; Reisenbichler and Rubin 1999; Levin et al. 2001; McGinnity et al. 2003; Brenner et al. 2012; Zhivotovskiy et al. 2012).

## Homing mechanisms

### Genetic effects

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, sexual 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 hatchery production, transplant projects, reintroductions, or efforts to establish new populations. An experiment using hatchery Chinook salmon (*O. tshawytscha*) by Hard and Heard (1999), for example, showed lower homing by adult fish whose parents' gametes had been transported to a hatchery than for fish whose parents had voluntarily returned to the hatchery, suggesting a genetic effect. Other circumstantial case studies have reported higher stray rates for hybrid Chinook (Candy and Beacham 2000) and pink salmon (Gilk et al. 2004). Hybrids in Candy and Beacham (2000) strayed at rates three times higher than those by the natal population released at the same location. The same study showed transplanted fish were more likely to stray to their ancestral river (despite never being exposed to the ancestral site) than control groups. Similarly, McIsaac and Quinn (1988) and Pascual and Quinn (1994) showed that adult Chinook salmon derived from hatchery-reared juveniles returned to their ancestral spawning areas (several hundred kilometers upstream) 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. Genetic markers in Tallman and Healey (1994), for example, indicated lower straying rates than mark-recapture studies of chum salmon (*O. keta*). In a steelhead (*O. mykiss*) genetics study, Narum et al. (2006b) concluded that out-of-basin strays likely had lower reproductive success than local populations. 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 or markers indicating a predisposition for homing versus straying has not been identified.

## Juvenile imprinting

Two competing hypotheses arose during the early research on salmon homing and each included olfaction (Brannon 1982). One was that adult fish 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 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 widely accepted as the primary 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 et al. 1986; Moore and Scott 1991; Courtenay et al. 1997, 2001). Thus the two mechanisms should be viewed as complementary rather than mutually exclusive.

### *What odors are used for imprinting?*

Combinations of organic and inorganic materials produce complex chemical mixtures in streams and other aquatic systems that can be unique at very fine spatial scales. The homing literature has frequently referred to these mixtures 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 materials examined 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). 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.

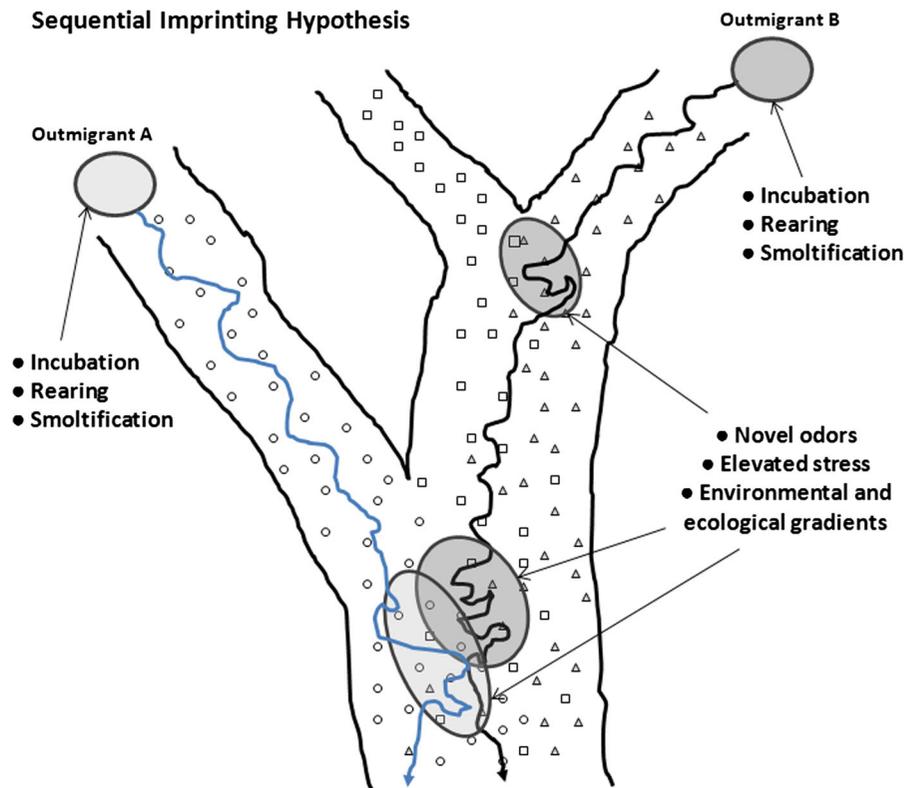
### *When does imprinting occur?*

Imprinting has been most associated with 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 below). However, sensitive periods differ among species and populations depending on life history and behavior. There is 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 [*O. nerka*] that spawn in tributaries to rearing lakes). Chinook salmon, coho salmon (*O. kisutch*) 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 the developmental window for imprinting time is relatively wide, does not occur as a single event, and that events are likely episodic for many species and populations, occurring at natal sites, rearing sites, along migration routes, and in response to proximate stimuli.

### *Multiple and 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

**Fig. 1** Examples of sequential imprinting by juvenile migrants. Olfactory imprinting occurs 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 facilitate imprinting at these sites



with changes in ecological and environmental conditions (Harden Jones 1968; Brannon 1982). The term is most often applied to imprinting during the course of juvenile outmigration (Fig. 1). Imprinting in a series of spatially discrete events near natal sites and 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 insight on this process. Transport studies of coho salmon (Solazzi et al. 1991) and Atlantic salmon (*S. salar*) (Gunnerød et al. 1988; Heggberget et al. 1991) 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 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 detect dilute olfactory signatures from small natal streams far downstream in well-mixed, high volume migration corridors or estuaries (Quinn 2005).

#### *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. These include hormonal activity controlled by the pituitary system, olfactory processes related to odor detection, 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; Dittman et al.

1997; Nevitt and Dittman 1999; Hino et al. 2009; Ueda 2011, 2012).

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 ( $T_3$ ). 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 is 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 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, 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 a greater propensity for straying in hatchery versus wild salmonids (Nishioka et al. 1985; Dittman and Quinn 1996; Björnsson et al. 2011).

Olfactory processes are controlled, at least in part, by olfactory receptor genes (Dukes et al. 2004; Hino et al. 2009). Johnstone et al. (2011) showed that olfactory genes were expressed differently among parr, smolts, and adults in anadromous Atlantic salmon. In contrast, a landlocked population showed no differences in which 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 landlocked salmon did not appear to require these processes and hence these genes were not upregulated (Johnstone et al. 2011). 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.

#### *Imprinting experiments*

Evidence supporting the role of olfaction in homing accumulated over an extended period starting in the 1950s. An influential 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 study fish was stable through time, an important requirement for homing salmonids given their years away from the natal site.

Hasler and his colleagues then embarked on a series of imprinting experiments using artificial odorants and coho salmon. They exposed juvenile salmon to the organic compounds morpholine or  $\beta$ -phenylethyl alcohol (PEA, Table 1) and then tested whether returning adults could be attracted to water sources with these chemicals (Wisby and Hasler 1954; Hasler 1966; Cooper and Hasler 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

**Table 1** Glossary of imprinting and olfaction

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*Term:* definition

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*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/T<sub>4</sub>/T<sub>3</sub>:* 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

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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 era, experiments tested the sensitivity of olfactory cells to both 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, 1994; Morin and Døving 1992; Dittman et al. 1996). Experiments using earlier life stages also showed that exposure to odorants would elicit a response several months later as parr (Dickhoff and Sullivan 1987; Courtenay 1989), though not necessarily as adults (Dittman et al. 1996). Importantly, the observation of a 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 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, 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; Bandoh et al. 2011). Longer exposure periods resulted in stronger imprinting, and brain imaging showed that adult recognition was associated with olfactory bulb activity.

#### Parr-smolt transformation and outmigration

The parr-smolt transformation (PST, synonymously referred to as ‘smoltification’, Table 2) is a hormone-driven developmental process that is cued by environmental change and especially by photoperiod and water temperature (Zaugg 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; 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 regard to imprinting. It is clear, however, that the suite of changes associated with migration and preparation

**Table 2** Glossary of parr-smolt physiology*Term: definition*

*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

for saltwater entry are intimately linked to olfaction and memory. The thyroid hormones associated with imprinting, for example, also influence morphological and pigmentation changes and 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  $Na^+K^+$ -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. Concurrent increases in growth hormones tend to accelerate the physiological changes of smoltification (McCormick 2009).

Importantly, the act of migration itself stimulates hormone production. In particular, thyroid and adrenal hormones spike as smolts encounter new environmental, ecological, and chemical stimuli. Behavioral changes, including the shift from positive to negative rheotaxis, are also mediated by anatomical and physiological changes. These multiple feedback loops

tied to outmigration strongly reinforce the association between PST and imprinting. Interrupting or preventing migration has been shown to negatively affect imprinting, and there are several examples of reduced adult homing when smolts were held in a hatchery during the PST (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.

## Hatchery rearing

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 relatively stable hatchery environments (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 reduce 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. Once released (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 often 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 differ 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 reduced imprinting near the release site. Overall, these results imply that there may be opportunities to improve homing of hatchery reared salmonids by: (1) increasing heterogeneity and complexity of experience in hatcheries to increase expression of imprinting hormones, and (2) by more closely matching release timing to natural PST timing.

### Adult homing

The remarkable adult migrations of anadromous salmonids 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 (Table 3). 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; Hansen et al. 1993; Dat et al. 1995; Lohmann et al. 2008; Bracis and Anderson 2012; Putman et al. 2013). Salmon may navigate using these same mechanisms in the near-shore ocean and in estuaries, along with orientation by visual and olfactory cues, and 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. Straying may occur between basins separated by marine habitats (e.g., between two coastal streams) or within a basin after return to freshwater, and mechanisms underlying these two types of events may differ. For instance, while it is clear that olfaction is the dominant orientation mechanism in late stages of

**Table 3** Glossary of adult homing and straying

*Term:* definition

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|   |  |
|---|--|
| <i>Chemotaxis:</i>  | orientation towards chemical cues, including olfactory cues  |
| <i>Cortisol:</i>  | stress hormone that controls an array of functions; associated with increased olfactory sensitivity in maturing salmonids  |
| <i>Estradiol:</i>   | estrogen hormone affecting reproductive functions and secondary sexual traits  |
| <i>Exploring/sampling/testing/proving/temporary straying:</i> | class of behaviors, often used synonymously, that characterize non-direct homing migrations and temporary use of non-natal sites along migration routes or near natal areas                |
| <i>Glucocorticoids:</i>                                       | group of steroid hormones that includes cortisol; affect immune system and metabolism  |
| <i>Gonadotropin:</i>  | pituitary hormone that controls growth, sexual development, and reproductive function  |
| <i>Guanylyl cyclase:</i>                                      | olfactory enzyme associated with odor recognition; maturing salmon show increased g-c sensitivity and it likely facilitates salmon homing  |
| <i>Homing:</i>  | adult return to natal site for reproduction; spatial scale can vary  |
| <i>Navigation:</i>  | ability to move from one location to another (i.e., homing) without prior information about the route; requires sense of direction and geographic position                                 |
| <i>Odor-conditioned rheotaxis:</i>                            | when animals use a combination of olfactory and rheotactic cues during movement; used for homing in complex environments   |
| <i>Orientation:</i>   | moving towards a stimulus, such as light, food, or odor; the physiological basis for navigation  |
| <i>Overshoot:</i>   | migration behavior where adults migrate past their natal river drainage and must move downstream to successfully home  |
| <i>Rheotaxis:</i>   | innate behavior where fish orient into the current (positive rheotaxis) or orient away from current (negative rheotaxis)   |
| <i>Senescence:</i>  | rapid aging with decline in immune function, organ and cell atrophy, starvation, elevated stress hormones; associated with maturation and post-reproduction death in semelparous salmonids |
| <i>Straying:</i>  | adult return to non-natal location for reproduction; spatial scale can vary  |

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freshwater migration (i.e., while approaching the natal site), the point at which adults switch to primarily olfaction from other orientation systems is unknown. While orientation and navigation in salt water is critically important for understanding large-scale homing behaviors, there has been limited empirical homing research in the oceans and we therefore focus

on adult homing during the freshwater phase of migration in the sections below.

### *Adult migration physiology*

Adult salmonids go through significant 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; Ueda 2011). Semelparous species also begin to senesce, typically starting with the cessation of feeding and including impaired immune function and 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 short-term memory, but they serve a variety of useful functions for maturing adults. In regard to homing, stress hormones can 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 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 1976; Hasler and Scholz 1983; Dittman et al. 1996).

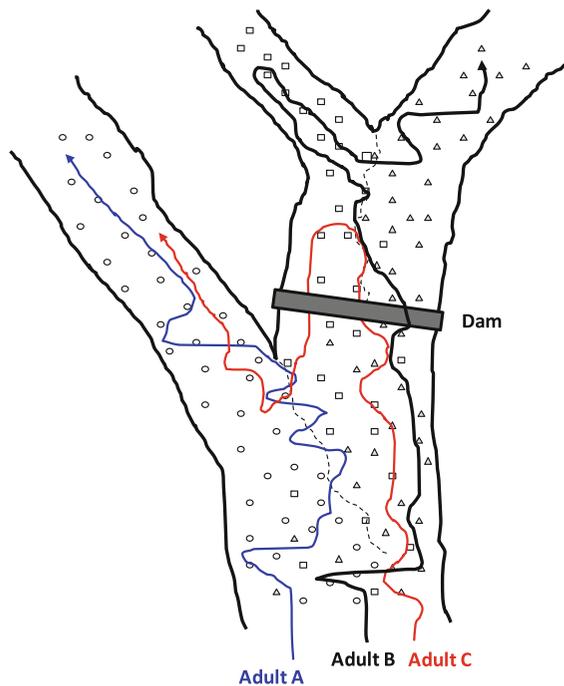
Iteroparous species experience essentially the same reproductive maturation processes as semelparous species, but senescence is regulated differently in individuals that survive post-spawning. Senescence in repeat spawners, or the lack thereof, may be genetically controlled or be associated with age, 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 homing migration 6–10 months prior to spawning and can hold for months at sites distant from natal areas (High et al. 2006; Keefer et al. 2008c, 2009). Lower reproductive hormone levels for ‘early’ migrants (like steelhead) that enter freshwater well before maturation suggest that they may have reduced olfactory sensitivity compared with those with more advanced maturation schedules or that olfactory sensitivity is affected by additional pathways.

### *Adult homing behavior: migration corridors*

Adult salmonids rely upon rheotactic and olfactory cues during upstream migration, a combination that is widely used by aquatic species and is 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 (Fig. 2). When the expected olfactory cues are diffuse

### Odor-conditioned Rheotaxis



**Fig. 2** Examples of odor-conditioned rheotaxis by homing adult migrants. *Open symbols* represent odor signals from three tributaries. Migrants (*lines*) 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 and B) or retreat downstream (example 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)

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.

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 fish (Døving and Stabell 2003). In rivers and estuaries, similar frequent but short-duration vertical movements have been reported for

several species (Olson and Quinn 1993; Johnson et al. 2005, 2010), and these behaviors presumably also facilitate olfactory sampling.

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

Impaired odor-conditioned orientation in the Columbia River has been demonstrated 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). Overshoot distances can be considerable (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 (Fig. 2). In less regulated rivers, overshoot behaviors by adult salmonids have also been reported on the scale of 10’s of kilometers and typically occur close to spawning areas (Heggberget et al. 1988; Thorstad et al. 1998; Økland et al. 2001).

#### *Adult homing behavior: exploration and testing*

Exploration of non-natal habitats appears to be to be an innate part of adult 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). Some of this behavior occurs at sites that are distant from natal areas in

response to environmental cues (Gonia et al. 2006; Keefer et al. 2009; Clarke et al. 2010, 2011). More commonly, exploring and sampling behaviors have been observed near spawning grounds, and typically include movements that range from hundreds of meters to 10's of kilometers (Griffith et al. 1999; Økland et al. 2006; Connor and Garcia 2006). Males appear more likely than females to move among potential spawning sites as they search for mates (Hard and Heard 1999; Neville et al. 2006; Anderson and Quinn 2007; Hamann and Kennedy 2012). Importantly, the relationship between exploration and failure to home is unclear. It is also unknown whether some individuals are genetically predisposed to test novel habitats or whether ecological context is the primary trigger for these behaviors.

## Developing a straying lexicon

### Challenge 1: Spatial scale

Straying is fundamentally a question of spatial classification, but the distinction between fish that home and those that stray is often far from clear. 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 interbreeding (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 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 discreet 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 at this spatial scale 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., Narum et al. 2006a, b, 2008; Dittman et al. 2010; Hamann and Kennedy 2012; Peacock and Holt 2012). This 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 less ambiguity about classifying strays as 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. 2008b) and when they spawn in geographically distant river systems (Labelle 1992; Unwin and Quinn 1993; Jonsson et al. 2003; Pess 2009; Leunda et al. 2013).

Defining spatial criteria for identifying hatchery strays can be especially difficult because behaviors can be influenced by ancestral source, hybridization, rearing and release strategies, transportation, inter-basin transfers, and a variety of other confounding factors. For instance, what criteria should be used to identify strays reared in one location (i.e., a central hatchery facility) but outplanted at one or more satellite locations (e.g., Candy and Beacham 2000; Schroeder et al. 2001) or 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 distributions. Similarly, it can be difficult to categorize 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).

### Challenge 2: Identifying strays

There are essentially two methods that have been used to identify strays: (1) marks or tags applied to juvenile fish (e.g., coded wire tags, PIT tags, fin clips, thermally induced otolith marks), and (2) inferred origin using genetic testing or otolith patterns. 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 low because some portion of the adult strays is not 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 (Mortensen et al. 2002; Dittman et al. 2010; Brenner et al. 2012) or in monitored fisheries (Youngson et al. 1997; Carmichael and Hoffnagle 2006; Clarke et al. 2010). However, selection of sampling reaches is rarely randomized, recovery effort among locations varies widely, and other potential sampling biases are rarely quantified.

An ideal estimate of straying *from* a population requires information on the final distribution of all adults from a cohort or return-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 or other methods. Recent advances in DNA fingerprinting and pedigree techniques (e.g., Thériault et al. 2011; Hess et al. 2012; Milot et al. 2013) may be applied to identify strays into recipient populations at locations where all adults can be sampled over several years. Sub-sampling techniques may be sufficient if samples are spatially and temporally representative of both the potential strays and the recipient population. Nonetheless, there are almost no published examples of complete-census straying studies.

#### Challenge 3: Donor versus recipient populations

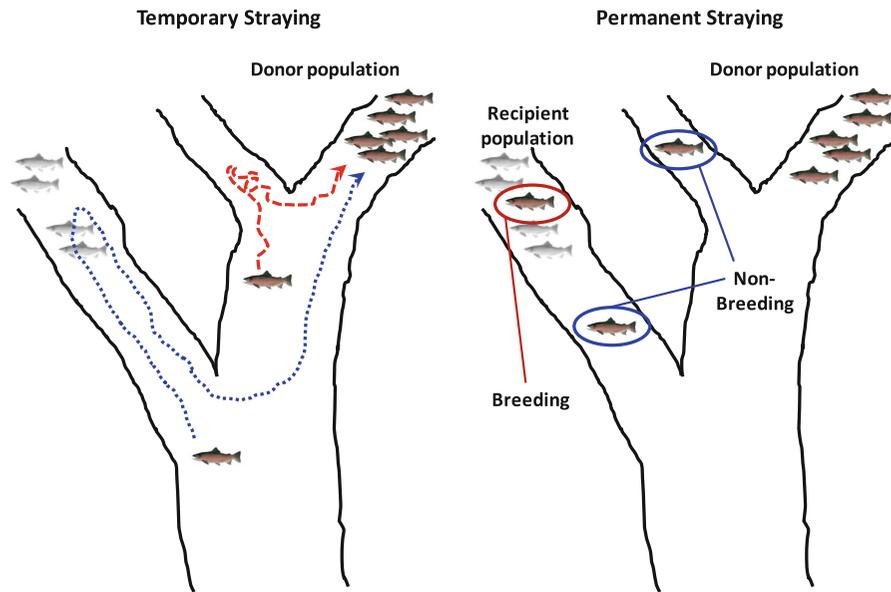
In our opinion, the straying literature has disproportionately reported on straying rates from donor populations and under-reported on straying into receiving populations. This has been an artifact, at least in part, of hatchery programs marking juvenile fish and strays being recovered and identified 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 Washington (Milks et al. 2006; Gallinat and Ross 2011), coho salmon in British Columbia (Labelle 1992), and steelhead in Oregon (Schroeder et al. 2001; Hand and Olson 2003; Ruzycski and Carmichael 2010).

#### Challenge 4: Permanent versus ‘temporary’ straying

Several adult behaviors and human interventions complicate the straying lexicon because they result in some—but not all—of the elements of straying. The 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 described above. The second element (spawning) can also be difficult to classify. With the exceptions of carcass surveys and some tagging studies, 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). Similarly, ‘strays’ identified via capture in fisheries may or may not have spawned at their natal sites had they survived (Carmichael and Hoffnagle 2006; Naughton et al. 2009; Clarke et al. 2011). The first element in the definition (migration) can be complicated by wandering, exploratory, and thermoregulatory movements (Fig. 3). These behaviors have been collectively—and perhaps inappropriately—referred to as ‘temporary straying’.

It can be particularly difficult to disentangle permanent straying from thermoregulatory behaviors in temperate regions. This distinction is prominent in the Columbia River basin, for example, where water temperatures in the migration corridor are often warmer than those preferred by adult migrants. In warm years, a majority of some summer steelhead populations temporarily enter non-natal Columbia River tributaries (High et al. 2006; Keefer et al. 2009; Clarke et al. 2011) as do significant numbers of fall Chinook salmon (Gonia et al. 2006). Differentiating permanent from temporary straying into these cool-water tributaries is confounded by interception fisheries that harvest thermoregulating migrants and by capture at hatchery facilities (Hand and Olson 2003). Additional fish are detected in the cooler non-natal sites but their fate with regards to straying is unknown or ambiguous.

A strictly-defined lexicon of straying behaviors that can be applied across species, populations, and geographic regions is almost certainly not feasible. However, a benchmark at one end of the straying continuum may be



**Fig. 3** 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. Permanent straying can result in either inter-breeding with the recipient population,

colonization, or reproductive failure. Permanent strays are always a demographic loss from the donor population and may be a demographic gain for the recipient population. Straying versus homing status can be ambiguous for fish captured at non-natal hatchery facilities or in fisheries in non-natal sites

breeding at a non-natal location with genetically unrelated conspecifics (i.e., a breeding permanent stray, Fig. 3). A second relatively unambiguous category could be permanent strays that breed with other strays, the behavioral 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 that breeding is prevented. Each of these categories has strays as a demographic loss from the donor population, but have varying demographic and genetic effects on the recipient population. The ambiguous, temporary behaviors associated with behavioral thermoregulation, wandering, and 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.

### Straying mechanisms

A variety of inter-related factors potentially determine whether an adult migrant 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 versus effects of human-influenced factors. In the following sections, we review the mechanisms that can elicit adult straying and attempt to differentiate biological and ecological processes from factors that are largely a result of human interventions. Often, the proximate physiological and behavioral mechanisms affecting fish are the same, but the causal mechanisms differ.

### Incomplete juvenile imprinting

Although complete imprinting failure is uncommon in wild or hatchery populations, incomplete juvenile imprinting certainly plays a role in adult straying. Incomplete imprinting on the natal site or along the emigration route may occur when hormone surges are insufficient to stimulate olfactory memories. This may be related to variation among individuals (i.e., in endocrine 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). As described in previous sections, reduced stimuli in hatchery fish have been associated with lower hormone levels (Dittman and Quinn 1996; McCormick et al. 2003) as well as lower olfactory activity and reduced brain development (Marchetti and Nevitt 2003) compared to wild fish. For these reasons—and probably others—hatchery fish are widely believed to have reduced imprinting relative to wild fish.

Incomplete imprinting also may occur when juvenile dispersal is unaccompanied by the requisite physiological development. For example, Hamann and Kennedy (2012) showed that pre-smolt movements away from natal sites led to higher local-scale straying by wild Chinook salmon adults. Similarly, species with short freshwater residence times (e.g., chum salmon) may have reduced imprinting opportunity compared with species with extended residence times like coho and Chinook salmon or steelhead.

Lastly, exposure to water-borne chemicals has been shown to inhibit imprinting. Pesticides, insecticides, heavy metals, and persistent organic pollutants can all retard the PST, reduce olfactory activity, and inhibit neural connectivity (Moore et al. 2007; Arkoosh et al. 2011).

#### Interrupted juvenile imprinting

Interrupted imprinting—in contrast with incomplete imprinting—is almost always associated with human interventions. These include hatchery practices such as inter-basin transfers and outplanting from central rearing facilities. Outplanted and transferred juveniles are typically 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.

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 accumulating evidence suggests that adult straying rates increase with longer juvenile transport distance (Solazzi et al. 1991; Keefer et al. 2008b; Marsh et al. 2012).

#### Adult sensory failure

Straying can 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. The experiments of Wisby and Hasler (1954) and others using anosmic adult salmon 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. The surge in stress hormones during this life stage stimulates some olfactory processes and enhances 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 an overwhelming majority of adults home rather than stray, the effects of senescence and maturation do not appear to routinely impair homing. Nonetheless, relationships between straying and senescent processes 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 salmonids are potentially affected by a variety of ambient chemical contaminants (reviewed by Klapat et al. 1992; Tierney et al. 2010). Several laboratory studies have demonstrated that exposure to sublethal levels of pesticides (Moore and Lower 2001), insecticides (Scholz et al. 2000), and heavy metals (Baldwin et al. 2011) can inhibit 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. Because the olfactory system is continuously linked to the aquatic environment, contaminants directly contact the epithelium and olfactory receptor cells. Therefore, even

low toxin concentrations may affect olfactory processing.

#### Adult memory failure

Several studies have found associations between adult age and stray rate, 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 younger fish. Several showed a relatively large age effect, with older adults straying at substantially higher rates than younger fish in both wild and hatchery populations. However, 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 or higher straying by younger fish (e.g., Hard and Heard 1999; Candy and Beacham 2000). The former found that younger Chinook salmon (measured by years at sea) strayed at higher rates than older fish. This result was driven, in part, by more abundant males in the younger age classes (including jacks) and higher straying by males versus females.

A general hypothesis for age-mediated straying is that older fish spend more time in the ocean away from their natal river system and hence are less able to 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 ideas have much 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 where juvenile size, age and release timing effects interact in complex ways with adult return rates and homing behaviors, often making interpretation difficult.

#### Density-dependent reproductive behaviors

Intra-specific and density-dependent effects can influence exploratory movements and sampling behaviors

by adults. For example, there is some evidence that homing 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), 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 chum and Chinook salmon populations 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). In these cases, local-scale straying may be driven by density-dependent reproductive behaviors. 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 to what degree mate-seeking movements occur at sites distant (e.g., 10's–100's of kilometers) from natal spawning areas.

#### Genetic and life-history effects

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 homing variation among species 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). The role of genetics in adult straying remains an open question and is an active research arena.

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. 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 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 traits also can produce phenotypically divergent adults (e.g., in migration timing, spawn timing, or morphological traits), and each of these factors also may contribute to stray rate variability (Lin et al. 2008). In a unique paired-release comparison of straying between life-history types, Westley et al. (2013) found that ocean-type Chinook salmon strayed at higher rates than stream-type Chinook salmon. The ocean-type salmon emigrate as subyearlings (often rearing for extended periods along the migration corridor), whereas most stream-type fish emigrate rapidly from natal sites as yearlings. These life-history differences implicate temporal and spatial effects on juvenile imprinting as predictors of adult homing outcomes (Westley et al. 2013).

#### Attraction to non-natal sites

The reason(s) that straying adults select one non-natal site over other available locations is not known, yet some recipient systems are clearly favored. Spatial proximity to the natal site is an important predictor, as many 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; Westley et al. 2013). Several 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 infrequent (Olsen et al. 2008). The authors attributed 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 similar physiochemical characteristics, especially when drainages are small (i.e., adjacent creeks), and this surely affects the spatial distribution of strays described above. Recent Chinook salmon research by Dittman et al. (2010) and Cram et al. (2013) showed how relatively local scale differences in spawning habitat quality affected the distribution of adults, with higher local straying when conditions at the home site were less favorable. Similar processes may occur at larger spatial scales, though little empirical evidence has been collected.

#### Synthesis of straying data

Although there is a large literature describing straying, it is 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 studies have had site-specific or experimental elements that confound direct comparisons across studies. Most often, some group(s) of fish were either transferred or outplanted to a site other than the rearing site or fish were reared at a location other than their ancestral site. Furthermore, one or more of the straying estimation challenges described above occurred in almost all empirical straying studies. For these reasons, the data presented in this section are likely biased high relative to straying in ‘natural’ populations with limited human interference. We caution against over-interpretation of any individual stray rate estimates in the summaries presented below.

We have emphasized Columbia River (USA) in the data synthesis because this intensively-managed, multi-species system has been the focus of many homing and straying studies. We have also restricted the presented data to anadromous chum, pink,

sockeye, coho and Chinook salmon and steelhead in the *Oncorhynchus* genus and Atlantic salmon in the *Salmo* genus. Most homing and straying research has focused on these species. Data from species for which anadromy is less frequently obligatory (e.g., *Salmo trutta*, *Salvelinus alpinus*, *Salvelinus fontinalis*, *Salvelinus malma*, *Oncorhynchus masou*, *Oncorhynchus Clarkii*, and others) were not included.

Sixty-two data sources were selected to provide a general summary of the types of straying information that have been collected in the Columbia River basin (Table 4) and at other representative sites throughout the current ranges of the study species (Table 5). These studies were a representative subsample, though we made an effort to include a range of project types (e.g., tagging studies, genetic studies, carcass surveys, etc.) and a variety of species. Literature for the synthesis was initially collected by searching the peer-reviewed database Web of Science and by searching grey literature reports by U.S. state and Federal resource agencies. We emphasized peer-reviewed documents over grey literature when possible but used agency studies when they included novel elements or reported on populations not described elsewhere.

Most straying estimates have relied on tagged fish, and especially on fish with coded wire tags. A variety of other marks have 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 inherent differences in stray rates among species and life-history types (Figs. 4, 5). Multi-species reviews by Hendry et al. (2004), Quinn (1993, 2005), Pess (2009), and Westley et al. (2013) generally align with the estimates we derived. 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 population straying rates than other species, on average. The lowest mean estimates were for stream-type Chinook salmon and sockeye salmon. Coho salmon, Atlantic salmon, and steelhead had intermediate mean values.

Studies that directly compared straying between species or between life-history types within a shared river system and migration year have been very uncommon. A few exceptions included the study of

winter steelhead and coho salmon by Shapovalov and Taft (1954) and several Columbia and Snake River studies, which typically included Chinook salmon (ocean-type or stream-type), coho salmon, sockeye salmon, and/or summer steelhead (e.g., Ebel 1980; Bjornn and Ringe 1984; Chapman et al. 1997; Keefer et al. 2008b; Marsh et al. 2012; Westley et al. 2013). Most of these studies relied on an aggregation of contributing populations, resulting in reduced inferential opportunity.

#### Donor population stray rates

##### *Chum and pink salmon*

There have been few studies of chum or pink salmon straying (Fig. 4), but the available data suggest that these species stray at relatively higher rates than other Pacific salmonids or Atlantic salmon (Quinn 1993; Hendry et al. 2004; Pess 2009). Field studies by Sharp et al. (1994), Tallman and Healey (1994), Wertheimer et al. (2000), and Small et al. (2009) all reported straying estimates of >10 % for chum or pink salmon. Reported straying was somewhat lower (~4–7 %) for Alaskan pink salmon in Mortensen et al. (2002), but a relatively small number of nearby sites were sampled for strays in this study. A consistent theme was that relatively unstable habitats across years, in combination with abundant suitable spawning habitat in close proximity to natal sites, allows many chum and pink salmon strays to successfully reproduce (i.e., there is little fitness cost for low philopatry).

##### *Sockeye salmon*

There has also been relatively little systematic straying research on sockeye salmon. The mean estimate from the small number of studies we reviewed was 2.4 % (Fig. 4). This was slightly higher than the 0.8 % reported by Pess (2009), but in the range of estimates for sockeye salmon in Quinn (1993) and Hendry et al. (2004). The genetic evaluation by Lin et al. (2008) of local-scale straying in an Alaskan population was also <5 %. Anecdotal reports from radiotelemetry studies by Naughton et al. (2005) and Keefer et al. (2008e) indicate that some sockeye salmon from the interior Columbia River basin stray into tributaries along the migration corridor. A transportation study by Chapman et al. (1997) also found that upper Columbia

**Table 4** Representative straying studies from the Columbia River basin, USA used in the data synthesis

| Study # | References                    | Species            | Location                       | Primary method(s) | Transfer/outplant | Barge/truck transport |
|---------|-------------------------------|--------------------|--------------------------------|-------------------|-------------------|-----------------------|
| 1       | Quinn and 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 and Carmichael (2010) | Steelhead          | John Day River                 | Carcass,PIT       |                   |                       |
| 9       | Gallinat and Ross (2011)      | Chinook            | Tucannon River                 | PIT, CWT          |                   |                       |
| 10      | Bumgarner and Dedloff (2011)  | Steelhead          | Tucannon River                 | PIT               |                   |                       |
| 11      | Hamann and 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 and Washougal rivers     | CWT               | Yes               |                       |
| 14      | McIsaac and Quinn (1988)      | Fall Chinook       | Columbia River hatcheries      | CWT               | Yes               |                       |
| 15      | Hayes and Carmichael (2002)   | Fall Chinook       | Umatilla and Snake rivers      | CWT               | Yes               |                       |
| 16      | Garcia et al. (2004)          | Fall Chinook       | Clearwater and 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 and 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 and 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                   |

**Table 4** continued

| Study # | References          | Species            | Location    | Primary method(s) | Transfer/outplant | Barge/truck transport |
|---------|---------------------|--------------------|-------------|-------------------|-------------------|-----------------------|
| 32      | Marsh et al. (2012) | Chinook, Steelhead | Snake River | PIT               |                   | Yes                   |

River sockeye salmon strayed into lower Columbia River tributaries at low rates. Murdoch et al. (2009) investigated local-scale sockeye salmon straying for a population released as parr from net pens in Lake Wenatchee (Washington). They concluded that net-pen fish were less able to imprint on a natal stream and consequently the distribution of adults among spawning areas differed between net-pen and naturally-reared fish.

#### *Coho salmon*

The mean donor population stray rate for coho salmon was 9.8 %, slightly higher than the 7.8 % mean reported by Pess (2009). Estimates for coho salmon were quite variable across populations, reflecting a wide range of methods and experimental groups. The British Columbia study by Labelle (1992) was one of the more comprehensive projects (*mean* straying = ~5 %) because it included multiple hatchery and wild populations monitored over several years. The California estimates by Shapovalov and Taft (1954) were at the high end of the range for coho salmon (*mean* = ~17 %), whereas hatchery populations in Lake Washington (Washington) were at the low end (<1 %; Quinn et al. 1989). The low straying in the latter study was for fish reared and released on site; stray rates were variable and higher for outplanted and transported fish.

Coho salmon projects in the Columbia River basin mostly included outplanted or transported hatchery fish. Vreeland et al. (1975) used coho salmon reared at Little White Salmon Hatchery (Washington) 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 two study years. McCabe et al. (1983) reported higher (though unquantified) straying by coho salmon that were transported in trucks from Klickitat Hatchery (Washington) compared with an on-site control group. Solazzi et al. (1991) found that

Columbia River coho salmon that were trucked as juveniles increasingly strayed as transport distance increased (see details in [Juvenile transportation effects](#) section below).

#### *Ocean-type Chinook salmon*

The mean donor population stray rate in the ocean-type Chinook salmon studies we reviewed was 34.9 %. This was higher than for any other species or life-history type, but there was also very high among-population variability and a variety of experimental groups (Fig. 4). The ocean-type Chinook salmon studies were primarily in the Columbia River basin, but were distributed across multiple tributary and hatchery populations. These included groups from the lower river (McIsaac and Quinn 1988; Pascual et al. 1995; Quinn et al. 1991), the Umatilla and Yakima rivers in the mid-Columbia (Hayes and Carmichael 2002), and several lower Snake River and Clearwater River hatchery groups (Bugert et al. 1997; Garcia et al. 2004; Keefer et al. 2005; Milks et al. 2006; Arnsberg et al. 2007). Median rates ranged from about 1 % in the control groups in McIsaac and Quinn (1988), to ~10 % in the coded wire tag study of Bugert et al. (1997), to more than 50 % by transplanted experimental groups released in the Umatilla River (Hayes and Carmichael 2002).

Ocean-type 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. Garcia et al. (2004) reported that radio-tagged fall Chinook salmon strayed at relatively high rates (*median* ~20 %) among spawning areas in the Clearwater River and Snake River (Idaho). These fish were reared and acclimated at several locations, and juvenile imprinting on rearing

**Table 5** Representative straying studies from non-Columbia River sites used in the data synthesis

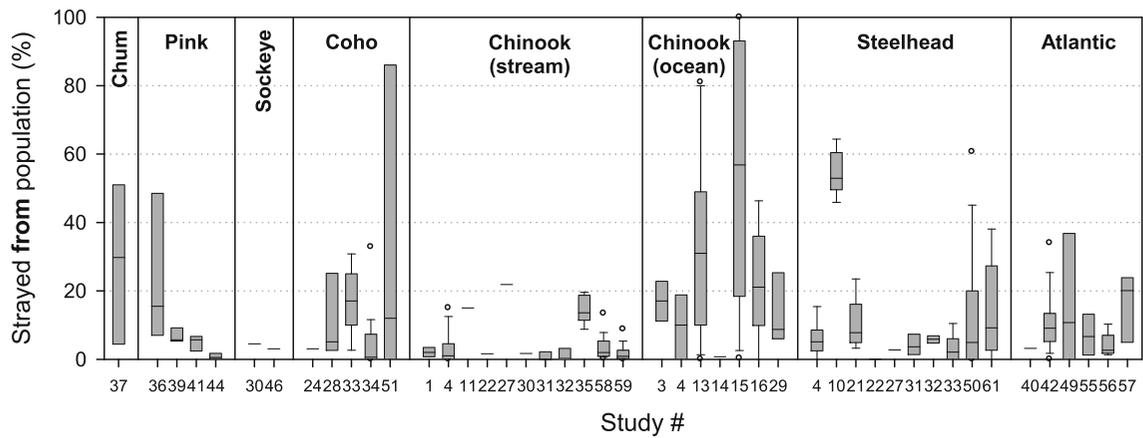
| Study # | References                       | Species             | Location         | Primary method | Transfer/<br>outplant | Barge/truck<br>transport |
|---------|----------------------------------|---------------------|------------------|----------------|-----------------------|--------------------------|
| 33      | Shapovalov and Taft (1954)       | Coho, Steelhead     | California       | Fin clips      |                       |                          |
| 34      | Labelle (1992)                   | Coho                | British Columbia | CWT            |                       |                          |
| 35      | Unwin and Quinn (1993)           | Chinook             | New Zealand      | CWT            |                       |                          |
| 36      | Sharp et al. (1994)              | Pink                | Alaska           | CWT            |                       |                          |
| 37      | Tallman and 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 and 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 and Hooton (1988)        | Steelhead           | British Columbia | CWT            | Yes                   |                          |
| 51      | Quinn et al. (1989)              | Coho                | Washington       | CWT            | Yes                   |                          |
| 52      | Johnson et al. (1990)            | Coho                | Oregon           | CWT            | Yes                   |                          |
| 53      | Hansen and Jonsson (1991)        | Atlantic            | Norway           | Tags           | Yes                   |                          |
| 54      | Slaney et al. (1993)             | Steelhead           | British Columbia | CWT            | Yes                   |                          |
| 55      | Hansen and 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 and Heard (1999)            | Chinook             | Alaska           | CWT            | Yes                   |                          |
| 59      | Candy and 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                   |                          |

sites likely contributed to adult straying patterns. About 4 % of the radio-tagged fall Chinook salmon in Keefer et al. (2005) strayed, with rates ranging from  $\leq 1$  % for hatchery fish released on site to  $>15$  % for salmon from the Yakima (Washington) and Umatilla (Oregon) rivers.

#### *Stream-type Chinook salmon*

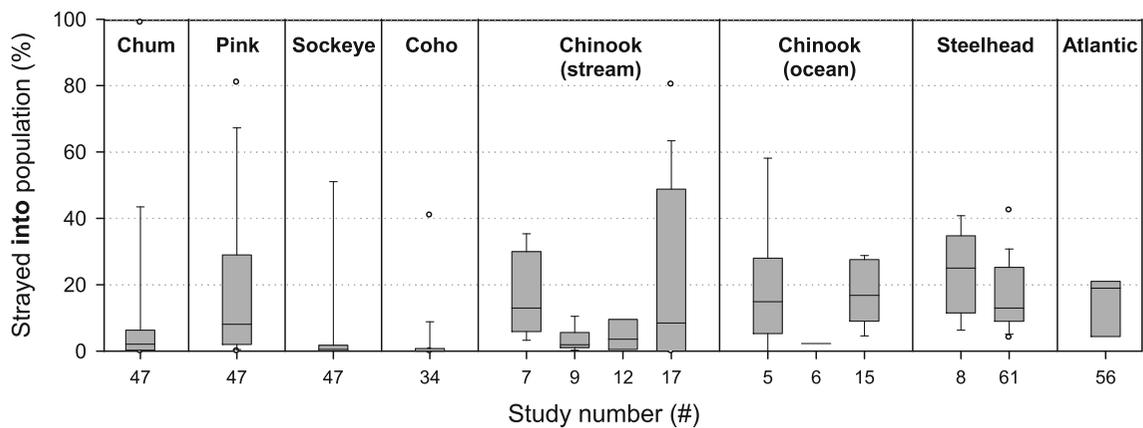
The mean donor population stray rate for stream-type Chinook salmon was 3.4 %, slightly lower than the 6.2 % mean reported by Pess (2009). Relatively low

straying was generally consistent across regions. For example, mean estimates were  $<5$  % in Hard and Heard (1999) and Candy and Beacham (2000), two well-designed and data-rich straying studies in Alaska and British Columbia, respectively. The somewhat 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. Estimates for Columbia River stream-type Chinook salmon have consistently been  $<5$  %, though some case studies have had estimates ranging to more than 20 %. The higher



**Fig. 4** Representative estimates of stray rates from donor populations (i.e., percentage that did not home to natal site). See Tables 4 and 5 for study numbers. Boxes show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Methods differed widely across studies and almost all included hatchery or experimental

groups, potentially resulting in higher rates than would typically occur in wild populations. However, all potential recipient populations were rarely monitored, potentially resulting in stray rate underestimation



**Fig. 5** Representative estimates of stray rates into recipient populations (i.e., percent of population made up of strays). See Tables 4 and 5 for study numbers. Boxes show 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. Methods differed widely across studies and almost all included hatchery or experimental

groups, potentially resulting in higher rates than would typically occur in wild populations. However, all potential donor populations were rarely monitored, potentially resulting in stray rate underestimation

estimates have generally been associated with small sample sizes, such as the Bjornn and Ringe (1984) Snake River transport study, 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 (Idaho) and the Yakima River (Washington) study by Dittman et al. (2010).

Stream-type Chinook salmon in the reviewed studies tended to stray into nearby rivers, particularly

in the absence of interventions like juvenile transport or hatchery outplanting. As examples, Cowlitz and Wind River (Washington) salmon mostly entered other lower Columbia River tributaries (Quinn and Fresh 1984; Keefer et al. 2005), South Fork Salmon River (Idaho) fish mostly strayed into non-natal tributaries within the South Fork drainage (Matala et al. 2012), and Willamette River (Oregon) salmon mostly strayed into nearby drainages within the Willamette basin (Schroeder et al. 2007).

In contrast, stream-type Chinook salmon transported as juveniles often strayed to more distant sites as adults. Salmon transported from the upper Columbia and Snake rivers, for example, typically strayed into tributaries in the lower and mid-Columbia River basin (Bjornn and Ringe 1984; Chapman et al. 1997; Keefer et al. 2008b; Marsh et al. 2012). Notably, these studies did not estimate straying to tributaries upstream from transportation collection sites and hence the contribution of more local-scale straying was not estimated.

### *Steelhead*

Mean donor straying estimates for steelhead (winter and summer combined) were 13.8 % in the studies we reviewed and 7.7 % in Pess (2009). This difference was attributable to the populations included in each summary. There was considerable variability among the studies we reviewed (Fig. 4). Some differences could be attributed to management or experimental protocols (e.g., outplanting, acclimation facilities, etc.) as well as to life-history traits. For example, coastal populations of winter steelhead appeared to stray at somewhat higher rates than interior summer-run populations, perhaps reflecting the local adaptation effects described by Olsen et al. (2008).

Estimates for winter steelhead ranged from ~4 % in California streams (Shapovalov and Taft 1954), to ~13 % in small British Columbia rivers (Lirette and Hooton 1988) and ~14 % in coastal Oregon streams (Schroeder et al. 2001). These studies had various levels of hatchery effects and transplanting. There have been more estimates for summer steelhead, particularly in the Columbia River system. These included straying by introduced summer-run fish into winter-run populations in the Willamette River, Oregon (Chilcote 2003; Kostow et al. 2003; Kostow and Zhou 2006). Summer-run estimates in the reviewed research were typically between 3 and 10 %, although some point estimates were considerably higher. The highest estimates ( $mean = 55\%$ ) were for Tucannon River (Washington) steelhead that overshot their natal river and were last recorded in the Snake River upstream (Bumgarner and Dedloff 2011). Similar overshoot patterns were reported for steelhead from Lyons Ferry Hatchery (Washington), many of which were also recovered far upstream in Snake River tributaries (Mendel and Schuck 1989).

The migratory behaviors and life history of summer steelhead may lead to more ambiguous homing outcomes than for some of the other species. In particular, the tendency for thermoregulatory behavior along migration routes and extended freshwater residency prior to spawning can result in considerable steelhead harvest in non-natal tributary fisheries. For example, the straying estimates presented for Grande Ronde River (Oregon) steelhead ( $mean = 11\%$ ,  $range = 4\text{--}25\%$ ) by Clarke et al. (2011) included many steelhead that were reported harvested in the Deschutes River (Oregon), several hundred kilometers downstream. Marsh et al. (2012) estimated that 4–9 % of PIT-tagged Snake River steelhead strayed into the Deschutes or John Day rivers (Oregon) and Ruzycski and Carmichael (2010) estimated that ~2–4 % of transported Snake River steelhead strayed into the John Day River; none of these estimates controlled for harvest (i.e., some fish considered strays may have returned to natal sites in the absence of harvest). For comparison, Keefer et al. (2008b) estimated that Snake River summer steelhead strayed into lower Columbia River tributaries at rates of 2–7 % (non-transported fish) and 7–9 % (transported fish), after excluding reported harvest in non-natal sites.

### *Atlantic salmon*

Mean donor straying estimates for Atlantic salmon were 10.1 % in the studies we reviewed and 7.7 % in Pess (2009). Many studies worldwide have included elements associated with pen-raised or hatchery-reared Atlantic salmon or have included juvenile transplant or transport as part of the study design. For example, point estimates of straying for populations in Newfoundland (Dempson et al. 1999), Norway (Gunnerød et al. 1988), Iceland (Isaksson et al. 1997), and the Baltic Sea (Vasemägi et al. 2005; Pedersen et al. 2007) have all exceeded 20 % in some years. Mean values have typically been lower (e.g., 4.4 % in Isaksson et al. 1997) and more similar to results for Chinook salmon. The River Imsa (Norway) straying study by Jonsson et al. (2003) provided one of the more thorough comparisons of straying by hatchery ( $mean = 15.4\%$ ) versus wild ( $mean = 5.8\%$ ) Atlantic salmon over multiple years. Annual estimates for the hatchery group ranged as high as 40 %, and these fish tended to stray to more distant river systems than wild fish.

## Recipient population stray rates

### *Pacific salmon*

Straying estimates into recipient populations have been uncommon relative to donor population estimates. However, there have been several recent recipient-based studies (Fig. 5). 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 (Alaska). In contrast, the coho salmon study by Labelle (1992) found consistently low (<5 %) stray rates into recipient populations on Vancouver Island, British Columbia.

In the Willamette River, Oregon, Schroeder et al. (2007) reported a wide range of recipient-based stray estimates for stream-type Chinook salmon. On average, ~23 % of the sampled fish were strays in various sub-basins and most were derived from nearby hatchery populations. Narum et al. (2008) used genetic assignments to identify stream-type Chinook salmon strays at four John Day River (Oregon) spawning sites and estimated that Snake River strays 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 than the estimates reported. In the Tucannon River (Washington) recipient population stray estimates have been made for stream- and ocean-type Chinook salmon (Milks et al. 2006; Gallinat and Ross 2011). On average, ~20 % of the ocean-type escapement and ~4 % of the stream-type escapement were strays. Sources included several regional populations. In the South Fork Salmon River (Idaho), Matala et al. (2012) cited mean recipient population stray rates of ~3–4 %, with the source population being a nearby hatchery.

### *Steelhead*

Recipient population straying estimates for winter steelhead have been limited. One exception was Schroeder et al. (2001), who estimated that hatchery winter steelhead strays made up 4–43 % of several winter steelhead populations in coastal Oregon rivers. Others have reported high (>50 %) recipient

population straying estimates of hatchery summer steelhead entering winter steelhead populations (e.g., Kostow et al. 2003).

Recipient population estimates for summer-run steelhead into other summer-run populations have been more common. For example, recipient-based straying was estimated in the Deschutes River (Oregon) by Hand and Olson (2003) and Carmichael and Hoffnagle (2006) and in the John Day River (Oregon) by Narum et al. (2008) and Ruzycki and Carmichael (2010). Hand and Olson (2003) showed that hatchery strays have accounted for >50 % of the total steelhead returns to Warm Springs River, a Deschutes River tributary. They also showed that annual counts of steelhead strays on the main Deschutes River ranged from several hundred fish in the early 1980s to more than 10,000 more recently. Using some of the same data sources, Carmichael and Hoffnagle (2006) estimated that strays made up <10 to >70 % of the Deschutes River steelhead run from 1977 to 2003. Origin hatcheries for these strays—when identifiable—were several hundred kilometers upstream in Snake River tributaries. A variety of methods were used to estimate straying in these studies, including counts, hatchery and trap recoveries, surveys in spawning areas, and harvest data.

In the John Day River (Oregon) a wild fish system with no hatcheries, Ruzycki and Carmichael (2010) observed thousands of hatchery summer steelhead strays 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; the vast majority originated in the Snake River. Similarly, a series of studies estimated straying by hatchery summer steelhead into Alpowa and Asotin creeks (Washington) had mean estimates of 46 and 11 %, respectively (Mayer et al. 2010; Crawford et al. 2012).

### Hatchery and outplanting effects

A recurrent pattern in the data synthesis was that juveniles that were either outplanted or transferred from their rearing location prior to release strayed at higher rates than those 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, and summer 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 (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 (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 (Hansen and Jonsson 1991; Candy and Beacham 2000).

#### Juvenile transportation effects

Several studies investigated the role of juvenile transportation on adult homing and straying, particularly in the Columbia River basin, where juvenile transportation is a primary mitigation strategy to reduce the effects of dams and reservoirs on survival. These studies typically used juveniles that were collected after they had volitionally begun downstream migration and therefore examined interrupted imprinting rather than incomplete imprinting. In cases where fish were fully removed from the migration route in trucks, there has often been very high straying (e.g., Johnson et al. 1990; Solazzi et al. 1991). Straying has also been higher—compared with control groups of in-river migrants—for fish that were transported downstream in fish barges (Vreeland et al. 1975; Ebel 1980; Bjornn and Ringe 1984; Ward et al. 1997; Schaller et al. 2007; Keefer et al. 2008b; Tuomikoski et al. 2011; Marsh et al. 2012) or with a combination of trucking and barging (Chapman et al. 1997).

The experimental coho salmon transport study by Solazzi et al. (1991) demonstrated that straying rate was

positively related to downstream transport distance. Straying to sites outside the Columbia River basin was <0.1 % for the on-site control group but was 3.4, 4.1, 6.1, 21.0, and 37.5 % for groups that were transported downstream ~205, 232, 253, 272, and 291 km, respectively. This distance effect was also evident in the Marsh et al. (2012) study of Snake River summer steelhead. They showed that juvenile steelhead barged to the Columbia River estuary (~600 km downstream from the collection site) strayed as adults at rates that were ~1.6–2.0 times higher than those that were barged to Bonneville Dam (~400 km downstream).

The weight of evidence suggests that juvenile transport affects adult orientation along the return migration route. Chapman et al. (1997) and Keefer et al. (2008b) reported higher rates of wandering and straying behaviors in the main stem Columbia River by transported fish, including fallback downstream past hydroelectric dams. The strays in these studies and in Marsh et al. (2012) were detected in multiple Columbia River tributaries, but particularly in the Deschutes and John Day rivers, corroborating results of high recipient population stray rates in those rivers (see above). Overall, there is growing consensus that transporting 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 stream-type Chinook salmon and larger for hatchery fish than wild fish. Patterns for ocean-type Chinook salmon and sockeye salmon have not been well described, although both Chapman et al. (1997) and Bugert et al. (1997) provided some evidence that transported fish strayed more than in-river controls. The combined research indicates that there are unexplained differences in stray rates among years that may be related to river conditions or to juvenile emigration timing and adult return timing. The juvenile effects presumably are related to physiological status or conditions experienced during transport. The adult effects may be related to either fish condition (e.g., maturation status) or environmental cues (e.g., conditions that prompt thermoregulatory behaviors).

Several studies have evaluated the physiology (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 (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 predators and 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—particularly in light of the variability among species, populations, and life-history types—will require considerably more work.

## Conclusions

### A need for quantitative analyses

As described above, the quantification of straying is challenging for many reasons. First and foremost, the physiology, life history, and behavioral ecology of salmonids are complex and interwoven with the expression of philopatry by individuals within populations and among species. There are certainly no universally ‘appropriate’ straying rates that can be used as management targets. Furthermore, estimating straying will continue to be logistically difficult for many populations because spawning habitats can be temporally and spatially dispersed, the events that influence homing outcomes occur over multiple life stages over multiple years, and identifying the natal origin of study animals is often impossible. For these reasons (and others), most future straying assessments will be driven by context-dependent constraints that require careful planning and analyses. Fisheries managers must balance the potential demographic and genetic risks of straying on both donor and recipient populations with the benefits of proposed management actions. This will require consideration of how strays are identified and enumerated, the size and spatial distribution of donor and recipient populations, and agreement about what stray rates are desirable or “natural”. Costs, benefits, and target rates are likely to differ widely among study systems.

In conclusion, the weight of evidence indicates that human activities—including many common fisheries, river management, and propagation practices—increase anadromous salmonid straying rates. Future research should strive to quantify these effects, clarify their ultimate and proximate mechanisms, and evaluate

their consequences for affected populations. We expect that the proliferation of genetic techniques will help researchers better measure dispersal and straying in unmanaged populations. Genetic data will also continue to provide quantitative insight into the widespread population-level effects of hatchery strays on their wild conspecifics. Common garden or paired-release experiments that explicitly compare imprinting- and homing-related mechanisms by hatchery versus wild fish are critically needed. Data from wild fish unaffected by hatchery rearing should help resolve many of the biological uncertainties that have hindered interpretation of previous homing and straying studies.

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