

Olfactory navigation during spawning migrations: a review and introduction of the Hierarchical Navigation Hypothesis

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ABSTRACT

Migrations are characterized by periods of movement that typically rely on orientation towards directional cues. Anadromous fish undergo several different forms of oriented movement during their spawning migration and provide some of the most well-studied examples of migratory behaviour. During the freshwater phase of the migration, fish locate their spawning grounds *via* olfactory cues. In this review, we synthesize research that explores the role of olfaction during the spawning migration of anadromous fish, most of which focuses on two families: Salmonidae (salmonids) and Petromyzontidae (lampreys). We draw attention to limitations in this research, and highlight potential areas of investigation that will help fill in current knowledge gaps. We also use the information assembled from our review to formulate a new hypothesis for natal homing in salmonids. Our hypothesis posits that migrating adults rely on three types of cues in a hierarchical fashion: imprinted cues (primary), conspecific cues (secondary), and non-olfactory environmental cues (tertiary). We provide evidence from previous studies that support this hypothesis. We also discuss future directions of research that can test the hypothesis and further our understanding of the spawning migration.

Key words: chemosensory, dispersal, electrophysiology, imprinting, *Oncorhynchus*, pheromones, philopatry, *Salmo*, salmon, trout.

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I. INTRODUCTION

Migrations are prevalent in a diverse array of species, including insects, birds, fish, amphibians, reptiles and mammals, and can provide insight into nearly all levels of life, from molecular to evolutionary (Dingle & Drake, 2007). While the term ‘migration’ encompasses a broad variety of behaviours, all migrations involve some form of persistent, directed and predictable movement, which occur on broad spatial and temporal scales, and often span multiple types of habitat (Aidley, 1981).

Many migratory species exhibit a specific form of migration known as natal homing, or movement to the natal location, which requires precise orientation capabilities. Orientation capabilities can be divided into three general categories (Ramenofsky & Wingfield, 2007): (i) compass orientation, in which movement occurs in a fixed direction and relies on the detection of large-scale cues (such as geomagnetic or celestial cues); (ii) true navigation, in which an animal’s position is determined by a cognitive map (established either genetically or through experience); and (iii) piloting, in which local cues such as landmarks or odours are used to provide direction. These categories of oriented movement are not mutually exclusive. For example, the combined use of compass orientation and cognitive maps has been well demonstrated in birds (Åkesson & Hedenström, 2007).

Anadromous fish are well known for their distinctive life histories: after hatching in fresh water, they migrate to the ocean to feed, and then return to fresh water to spawn. As the fish progress through their different life stages, they utilize different types of oriented movement. In salmonids, the best-studied group of anadromous fish, the outward ocean migration appears to rely at least partially on compass orientation (Putman *et al.*, 2014). The return or spawning migration, meanwhile, can be divided into two distinct phases. First, the fish must navigate the open ocean, possibly through compass orientation (Harden Jones, 1968; Putman *et al.*, 2013). Second, upon reaching fresh water they use olfactory cues to locate their upstream spawning grounds through piloting.

Herein, we provide an overview of how olfaction is used during spawning migrations, synthesize past research that explores this topic, and conduct a comprehensive assessment of our current understanding. We then discuss limitations in the research as a whole and provide directions for investigation that will help fill our existing knowledge gaps. Finally, we propose a new hypothesis for natal homing that reconciles the two hypotheses that currently dominate this field of work.

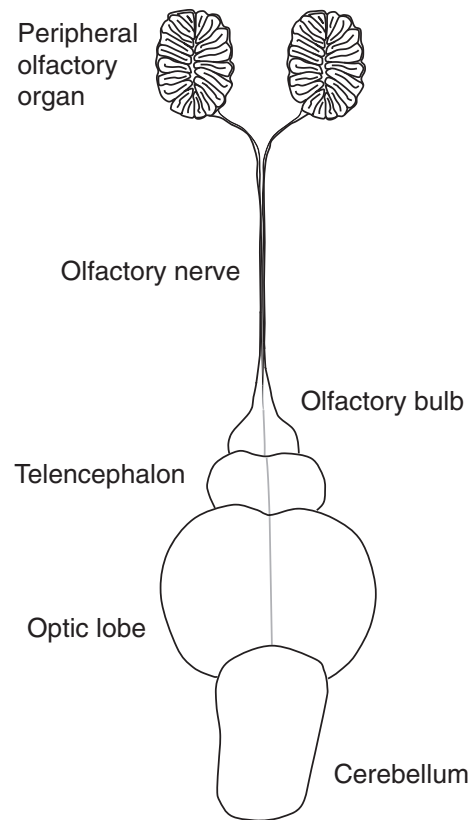


Fig. 1. Dorsal view of the olfactory system in a salmonid. The peripheral olfactory organs are covered with the olfactory epithelia and are directly exposed to the surrounding water (Hara, 1992). Odorants bind to G protein-coupled receptors in the olfactory epithelium, which leads to the formation of a secondary messenger and the opening and closing of various ion channels. As ions pass through the channels, there is a change in the membrane potential that triggers an action potential. The action potential travels along the axons of the olfactory sensory neurons, which form synaptic contacts with mitral cells in the olfactory bulb. The mitral cells project to the brain, where the information is processed.

II. USE OF OLFACTION DURING THE SPAWNING MIGRATION

The freshwater phase of the spawning migration relies primarily on olfaction (Hasler & Scholz, 1983; Dittman & Quinn, 1996), and the physiology of the olfactory system in fish has been reviewed extensively (Hara, 1994; Hamdani & Døving, 2007; Zielinski & Hara, 2007). The process begins at the peripheral olfactory organ(s), where odorants bind to receptors in the olfactory epithelia, and a signal is transmitted through the olfactory nerve to the olfactory bulb (Fig. 1). These signals generate responses in different regions within the bulb, which vary with the chemical identity of the stimulant (Morin & Døving, 1992; Laberge & Hara, 2004). Chemical cues that signify the spawning destination are

then interpreted in the brain, although the manner in which this information is processed has not yet been elucidated.

There are over 150 species of anadromous fish (Reide, 2002), and the majority are philopatric, returning to their natal tributary to spawn. Such 'natal homing' migrations have been most extensively studied in salmonids, and there are two primary hypotheses that seek to explain how natal homing occurs. The Olfactory Imprinting Hypothesis (Hasler & Wisby, 1951; Hasler, Scholz & Horrall, 1978) proposes that juveniles imprint on the unique odours of their natal tributary and then migrate towards these imprinted cues as adults. Harden Jones (1968) expanded on this hypothesis, suggesting that migrants not only imprint on natal water, but also on multiple 'waypoints' during the out-river migration. Returning adults then direct themselves towards these waypoints in the reverse sequence. A second hypothesis is the Pheromone Hypothesis (Nordeng, 1971), which proposes that adults migrate towards pheromones emitted from juveniles of the same population that are living in the natal water.

Some other anadromous fish, like lamprey (Petromyzontidae), are not philopatric, and do not return to their natal water to spawn (Waldman, Grunwald & Wirgin, 2008; Spice *et al.*, 2012). Instead, adults migrate towards chemical cues released by larval conspecifics (Moser *et al.*, 2015), with a preference for higher densities of larvae (Moore & Schleen, 1980. Limited dispersal at sea, however, restricts their migration and spawning distribution to the same broad geographical area in which they were hatched (e.g. the west coast of North America; Spice *et al.*, 2012). This type of migration strategy may be referred to as 'non-specific homing', which implies that migratory adults return to a general 'home' area, but not necessarily their natal tributary. A generalized attraction to pheromones is found in other migratory species of fish as well, such as in the family Galaxiidae (Baker & Hicks, 2003).

These two groups of fish – salmonids and lamprey – comprise the overwhelming majority of research on olfactory navigation during the spawning migration, and are therefore the focus of this review. There are many aspects within this field of work, including molecular processes, the identification and interpretation of olfactory cues, and the effects of endogenous and exogenous factors, that remain largely unknown. The following review synthesizes the research that has been conducted to date, and highlights the gaps in our knowledge.

III. A REVIEW OF OLFACTION AND THE SPAWNING MIGRATION

We conducted a comprehensive search of the peer-reviewed literature in ISI *Web of Knowledge* and

Aquatic Sciences and Fisheries Abstracts to identify studies that relate olfaction to migration in anadromous fish. We used the following topic search terms: 'olfact* AND (homing OR migrat* OR selection OR spawn* OR navigat*)' in conjunction with the names of 171 known anadromous species (K. Reide, personal communication). A total of 248 relevant papers were collected. The search was supplemented by the inclusion of studies that did not appear in our search results but were cited in the collected papers. There is a broad range of research that falls within our focal topic, and to synthesize this work we grouped the studies into the following six categories, based on their specific aims: (1) detection of spawning grounds through sensory systems; (2) responses to natal water; (3) responses to conspecifics; (4) responses to specific chemical compounds; (5) olfactory imprinting; and (6) molecular ecology of olfaction and the spawning migration.

(1) Detection of spawning grounds through sensory systems

Perhaps the most basic form of spawning migration research has focused on the relative importance of olfaction and other sensory systems in the detection of spawning grounds. These studies typically follow a similar methodology, in which the sensory systems of adult migrants are ablated, and their subsequent migratory behaviour is monitored. In most cases, impairment of the olfactory system significantly reduced homing success, whereas visual impairment had a more limited impact, such as increasing the time taken to reach natal water (Table 1). The earth's geomagnetic field may be a crucial component to the oceanic phase of the spawning migration (Putman *et al.*, 2014), such as the detection of natal river mouths (Putman *et al.*, 2013), although there is evidence that suggests otherwise (Yano *et al.*, 1996). In fresh water, studies on geomagnetic cues are limited, although they do not appear critical to the detection of spawning grounds (Ueda *et al.*, 1998). The critical role of olfaction to the spawning migration in anadromous fish is now widely accepted, and recent studies rarely involve sensory impairment.

(2) Responses to natal water

Many studies have focused on the responses, from cellular to behavioural levels, that are triggered by exposure to natal water (Table 2). Cellular responses to natal water have been identified in the olfactory bulb of sock-eye salmon (*Oncorhynchus nerka*; Bodznick, 1978a), and magnetic resonance imaging has revealed that exposure to natal water induces an increase in blood perfusion to certain regions of the telencephalon (Bandoh, Kida & Ueda, 2011). In addition, behavioural experiments and electrophysiology studies (which monitor electrical activity in the olfactory system) indicate that salmonids and alewives (*Alosa pseudoharengus*) are attracted to natal

Table 1. Importance of sensory systems to successful migration to spawning grounds

Reference	Species	Olfaction important?	Vision important?	Notes
Bertmar & Toft (1969)	<i>S. salar</i>	Y	—	—
Brett & Groot (1963)	<i>O. clarkii</i>	—	N	Blind fish located spawning grounds, but took longer
Dodson & Leggett (1974)	<i>A. sapidissima</i>	Y	Inconclusive	Site of release affected blind fishes' ability to locate spawning grounds
Groves, Collins & Trefethen (1968)	<i>O. tshawytscha</i>	Y	N	—
Hansen, Døving & Jonsson (1987)	<i>S. salar</i>	Inconclusive	—	Control fish did not successfully home either
Hiyama <i>et al.</i> (1966)	<i>O. keta</i>	Y	N	Sample sizes too small to determine statistical significance
Jahn (1969)	<i>O. clarkii</i>	Y	Inconclusive	—
Lorz & Northcote (1965)	<i>O. nerka</i>	Inconclusive	Inconclusive	No control for effect of sensory impairment
McCleave & Horrall (1970)	<i>O. clarkii</i>	—	N	Blind fish took longer to locate spawning grounds
McCleave (1967)	<i>O. clarkii</i>	Inconclusive	N	Many of the nare plugs did not stay in place
Rehnberg <i>et al.</i> (1985b)	<i>O. kisutch</i>	Y	—	Tested avoidance response to 10 ⁻⁶ M L-serine, did not avoid when anosmic
Ueda <i>et al.</i> (1998)	<i>O. nerka</i>	—	Inconclusive	Effect not significant, but blind fish took longer to locate spawning grounds. Impaired geomagnetic sensing had no effect
Vrieze, Bjerselius & Sorensen (2010) and Vrieze, Bergstedt & Sorensen (2011)	<i>P. marinus</i>	Y	—	—
Wisby & Hasler (1954)	<i>O. kisutch</i>	Y	—	—

Species: *Alosa sapidissima*, American shad; *Oncorhynchus clarkii*, cutthroat trout; *O. keta*, chum salmon; *O. kisutch*, coho salmon; *O. nerka*, sockeye salmon; *O. tshawytscha*, Chinook salmon; *Petromyzon marinus*, sea lamprey; *Salmo salar*, Atlantic salmon. Y, yes; N, no.

water, or respond to it more strongly than to other water sources (Hara, Ueda & Gorbman, 1965; Ueda, Hara & Gorbman, 1967; Thunberg, 1971; Sutterlin & Gray, 1973; Kaji *et al.*, 1975; Ueda, 1985; Sato, Shoji & Ueda, 2000). In coho salmon (*O. kisutch*) and Chinook salmon (*O. tshawytscha*), the natal water can be diluted down to 10% with little effect on the magnitude of the electrophysiological response (Hara *et al.*, 1965; Ueda *et al.*, 1967). The behavioural response is even more sensitive: Atlantic salmon (*Salmo salar*) are attracted to natal water that has been diluted to 0.1% (Sutterlin & Gray, 1973), and sockeye salmon show a preference for pure natal water over natal water that has only been slightly diluted to 90% (Fretwell, 1989). Interestingly, Sato *et al.* (2000) tested the electrophysiological response of lacustrine sockeye salmon to various waters collected from their natal pond and other regions of the same watershed, and found that the response to the pond water was the strongest, while the response to the water flowing into the pond was the weakest.

(3) Responses to conspecifics

In addition to natal water, anadromous fish also respond to water that is conditioned by conspecifics, which are other individuals of the same species (Table 3). An attraction to larval conspecifics has been demonstrated in several lamprey species, including sea lamprey (*Petromyzon marinus*; Teeter, 1980; Li & Sorensen, 1997; Vrieze & Sorensen, 2001; Fine, Vrieze & Sorensen, 2004; Sorensen *et al.*, 2005; Wagner, Twohey & Fine, 2009; Fine & Sorensen, 2010), silver lamprey (*Ichthyomyzon unicuspis*; Fine *et al.*, 2004), river lamprey (*Lampetra fluviatilis*; Gaudron & Lucas, 2006), and Pacific lamprey (*Entosphenus tridentatus*; Yun *et al.*, 2011). Regional panmixia in sea lamprey (Waldman *et al.*, 2008) and Pacific lamprey (Spice *et al.*, 2012) suggests that they are not philopatric, and therefore do not appear to use population-specific odours as spawning migration cues. As a result, few studies have attempted to determine whether lamprey respond similarly to larvae from different locations. There is evidence, however, that they

Table 2. Responses to natal water in anadromous fish

Reference	Species	Life-history stage	Reference water/chemical	Method	Response (relative to reference)	Additional results/notes
Bandoh <i>et al.</i> (2011)	<i>O. nerka</i>	Maturing adult	L-serine	MRI	Positive	Strongest responses (blood perfusion) in lateral area of dorsal telencephalon
Bodznick (1975)	<i>O. nerka</i>	Migrating and spawning adult	Other lakes and spawning grounds, ground water	E	Neutral	Did not respond more strongly to natal water than other spawning grounds. En-route migrants responded more strongly to natal water and other spawning grounds than completed migrants
Bodznick (1978b)	<i>O. nerka</i>	Parr	Other rivers	CR	Neutral	Responses to lake water similar to responses to CaCl ₂
Fagerlund, McBride & Smith (1963)	<i>O. nerka</i>	Migrating adult	Connected rivers, other spawning grounds	BA	Positive	Response to lake outlet stronger than response to inlets. Decreased response to volatile fraction, indicating volatile and non-volatile fractions both important to recognition
Fretwell (1989)	<i>O. nerka</i>	Migrating adult	Diluted natal water	BC	Positive	Preference for pure natal water over natal water diluted to 90%
Hara <i>et al.</i> (1965)	<i>O. kisutch</i> , <i>O. tshawytscha</i>	Spawning adult	Other lakes, hatchery	E	Positive	Response to natal water maintained when diluted to as low as 10%
Idler <i>et al.</i> (1961)	<i>O. nerka</i>	Migrating adult	Other lakes and rivers	BA	Positive	Increased response to inlets of natal lake that have spawning populations, but not to inlets without spawning populations or to other spawning grounds. Response to volatile fraction, but not to non-volatile
Kaji <i>et al.</i> (1975)	<i>O. keta</i>	Migrating adult	Other rivers	E	Positive	Different (but not necessarily 'stronger') response to natal water than other waters
Keefe & Winn (1991)	<i>S. fontinalis</i>	Migrating adult, parr	Other rivers Ground water	BC	Neutral Positive	No preference for natal water over other rivers Plugged nares of juveniles and made same choices when re-tested, suggesting gustation may be involved
McBride <i>et al.</i> (1964)	<i>O. nerka</i>	Smolt	Other nursery lake	BA	Positive	Smolts conditioned to respond more strongly to either own nursery lake or other lake
Oshima, Hahn & Gorbman (1969b)	<i>O. tshawytscha</i>	Spawning adult	Other rivers	E	Positive/ neutral	Response to natal water greater than two other waters, but similar to a third water
	<i>O. kisutch</i>	Spawning adult	Other rivers	E	Positive/ neutral	Increased response to natal water for one population tested, but not for other population
	<i>O. tshawytscha</i>	Smolt	Other rivers	E	Positive	Held in artificial salt water for 2 weeks prior to tests

Table 2. Continued

Reference	Species	Life-history stage	Reference water/chemical	Method	Response (relative to reference)	Additional results/notes
	<i>O. tshawytscha</i>	Smolt	Other river	E	Neutral	Held in aquaria, and after 3 days developed similar electrophysiological response to holding water as natal water
Oshima, Gorbman & Shimada (1969a)	<i>O. tshawytscha</i>	Spawning adult (jack)	Other hatcheries	E	Inhibited	Injected with memory-blocking agents (antimetabolites), which temporarily inhibited natal water discrimination (4–7 h)
Sato <i>et al.</i> (2000)	<i>O. nerka</i>	Spawning adult	Other lakes and rivers	E	Positive/neutral	Stronger response to natal water than all other waters except for water that fish had been held in for 1 week prior to tests
	<i>O. masou</i>	Spawning adult	Connected rivers and lake, other hatchery	E	Positive	—
Sutterlin & Gray (1973)	<i>S. salar</i>	Spawning adult	Downstream river	BC	Positive	Attracted to natal water diluted to 0.1%. Adding copper to natal water generated an avoidance response
Thunberg (1971)	<i>A. pseudo-harengus</i>	Spawning adult	Other lakes	BC	Positive	—
Ueda <i>et al.</i> (1967)	<i>O. kisutch</i> , <i>O. tshawytscha</i>	Spawning adult	Other spawning grounds and rivers	E	Positive	Response to natal water maintained when diluted as low as 10%
Ueda (1985)	<i>O. keta</i>	Migrating adult	Other rivers	E	Positive	Lower frequency responses only when exposed to natal water. Response to nonvolatile fraction, but not to volatile

Species: *Alosa pseudoharengus*, alewife; *Oncorhynchus keta*, chum salmon; *O. kisutch*, coho salmon; *O. masou*, masu salmon; *O. nerka*, sockeye salmon; *O. tshawytscha*, Chinook salmon; *Salmo salar*, Atlantic salmon; *Salvelinus fontinalis*, brook trout.

Methods: BA, behavioural assay; BC, behavioural choice; CR, olfactory cellular response; E, electrophysiology; MRI, magnetic resonance imaging.

can be attracted to larvae of different lamprey species (Fine *et al.*, 2004).

The effect of conspecific cues on the migratory behaviour of salmonids is less clear. A variety of different study methods, including field experiments, electrophysiology, and behavioural trials, suggest they are able to detect and respond to conspecific odours that emanate from faeces, bile, intestinal content, urine, and skin mucus (Døving, Enger & Nordeng, 1973; Hara & Macdonald, 1976; Selset & Døving, 1980; Stabell, Selset & Sletten, 1982; Courtenay, Quinn & Dupuis, 1997). If these odours are used as directional cues during natal homing, however, adults must be able to differentiate their own population from other populations. There is evidence that salmonids are capable of

population-level discrimination (McBride *et al.*, 1964; Nordeng, 1971, 2009; Døving, Nordeng & Oakley, 1974; Selset & Døving, 1980; Groot, Quinn & Hara, 1986; Quinn & Tolson, 1986; Courtenay *et al.*, 1997; Nordeng & Bratland, 2006), and even discrimination of siblings from non-siblings (Quinn & Busack, 1985; Quinn & Hara, 1986; Winberg & Olsén, 1992). It should be noted, however, that the results in some of these studies are at least partially inconclusive. For example, Groot *et al.* (1986) found population discrimination in one population but not in another, and Courtenay *et al.* (1997) found that coho fry of some populations appeared generally more attractive than fry of other populations. There is also contrary evidence that discrimination

Table 3. Response to conspecific cues (C.C.) and ability to discriminate populations in anadromous fish

Reference	Species	Life-history stage	Attractants	Method	Response/ attraction to C.C.? [*]	Pop. discr. [?]	Notes
Bjerselius <i>et al.</i> (2000)	<i>P. marinus</i>	Migrating adult	Larva	BC	Y	—	—
			Bile acids (larva)		Y	—	—
Black & Dempson (1986)	<i>S. alpinus</i>	Spawning adult	Larva	F	N	—	—
		Migrating adult	Adult and parr		N	—	Returned to homestream rather than tributary where fish from same population held
Brannon & Quinn (1990)	<i>O. kisutch</i>	Migrating adult	Adult and parr	F	N	—	Returned to homestream rather than hatchery where fish from same population held
Courtenay <i>et al.</i> (1997)	<i>O. kisutch</i>	Fry	Fry	BC	Y	Y/N	Prefer own population, but prefer other population if concentration higher
			Faeces (fry)		Y	Y/N	Some showed preference for own population, others did not
Courtenay <i>et al.</i> (2001)	<i>O. kisutch</i>	Fry	Fry	BC	Y	Y	Preferred siblings over non-siblings
Dizon, Horrall & Hasler (1973)	<i>O. kisutch</i>	Migrating adult	Adult	E	Y	—	Stronger response to homestream water with conspecific cues than without
Døving <i>et al.</i> (1973)	<i>S. alpinus</i>	Adult [†]	Adult	E	Y	N	—
			Urine, skin mucus (adult)		Y	—	Strongest response to skin mucus
Døving <i>et al.</i> (1974)	<i>S. alpinus</i>	Migrating adult	Fry	CR	Y	Y	Variation in response to different populations
			Mucus (fry)		Y	—	—
Fine & Sorensen (2010)	<i>P. marinus</i>	Migrating adult	Larva	BC	Y	—	—
Fine <i>et al.</i> (2004)	<i>P. marinus</i>	Migrating adult	Larva	BC	Y	—	—
			(<i>L. appendix</i> , <i>I. fossor</i>)		Y	—	—
	<i>I. unicuspis</i>	Migrating adult	Larva (<i>P. marinus</i>)		Y	—	—
Fisknes & Døving (1982)	<i>S. salar</i>	Subadult/adult [†]	Urine, intestine, mucus	E	Y	N	Strongest response to intestinal content
Gaudron & Lucas (2006)	<i>L. fluviatilis</i>	Migrating adult	Larva	BC	Y	—	—
Groot <i>et al.</i> (1986)	<i>O. nerka</i>	Migrating adult	Adult	BC	Y/N	Y/N	One population attracted to conspecifics and preferred its own population over another, other population showed no attraction or discrimination
			Adult and smolt	E	Y	Y/N	
Hara & Macdonald (1976)	<i>O. mykiss</i>	Subadult/adult [†]	Mucus Mucus (<i>C. clupeiiformis</i> , <i>C. auratus</i>)	E	Y Y	— —	— —
Keefe & Winn (1991)	<i>S. fontinalis</i>	Fry, migrating adult	Fry	BC	Y	N	Preferences persisted in anosmic fish, suggesting non-olfactory source
McBride <i>et al.</i> (1964)	<i>O. nerka</i>	Smolt	Smolt	BA	Y	Y	—
Nordeng & Bratland (2006)	<i>S. alpinus</i> , <i>S. trutta</i>	Migrating adult	Fry	F	Y	Y	Returned to homestream after transport as juveniles
Nordeng (1971)	<i>S. alpinus</i>	Migrating adult	Fry	F	Y	Y	Returned to homestream after transport as juveniles

Table 3. Continued

Reference	Species	Life-history stage	Attractants	Method	Response/ attraction to C.C.?:*	Pop. discr?	Notes
Nordeng (2009)	<i>S. alpinus</i>	Migrating adult	Fry	F	Y	Y	Returned to homestream after transport as juveniles
Quinn & Busack (1985)	<i>O. kisutch</i>	Fry	Fry	BC	Y	Y	Prefer siblings over unfamiliar non-siblings
Quinn & Hara (1986)	<i>O. kisutch</i>	Fry	Fry	BC	Y	Y	Preference for siblings, but discrimination appears to be learned, not innate
Quinn & Tolson (1986)	<i>O. kisutch</i>	Fry	Fry	E	Y	—	—
		Migrating jacks		BC	Y	Y	—
		Spawning adult			—	N	—
Quinn <i>et al.</i> (1983)	<i>O. kisutch</i>	Migrating adult	Fry	BC	Y	N	—
Selset & Døving (1980)	<i>S. alpinus</i>	Adult†	Smolt	BC	Y	—	—
			Intestine, mucus		Y	Y	Response to intestinal content and bile, but not skin mucus
Siefkes & Li (2004)	<i>P. marinus</i>	Migrating/ spawning adult female	Larva and spawning adult male	E	Y	—	—
Sorensen <i>et al.</i> (2005)	<i>P. marinus</i>	Migrating adult	Bile acids (larvae)	BC	Y	—	—
Stabell <i>et al.</i> (1982)	<i>S. salar</i>		Intestine mucus, (parr)	M	—	Y	Chemical composition of skin mucus and intestinal content different between populations
Sveinsson & Hara (2000)	<i>S. alpinus</i>	Adult	—	E	Y	—	—
Teeter (1980)	<i>P. marinus</i>	Migrating adult	Larva	BC	Y	—	—
Vrieze & Sorensen (2001)	<i>P. marinus</i>	Migrating adult	Larva	BC	Y	—	—
		Subadult			N	—	—
Wagner <i>et al.</i> (2009)	<i>P. marinus</i>	Migrating adult	Larva	F	Y	—	—
Winberg & Olsén (1992)	<i>S. alpinus</i>	Parr	Fry	BC	Y	Y	Prefer siblings over unfamiliar non-siblings
Yun <i>et al.</i> (2011)	<i>E. tridentatus</i>	Migrating adult	Larva	BC	Y	—	—
			Bile acids (larva)	E	Y	—	—
Zhang <i>et al.</i> (2001)	<i>S. namaycush</i>	Subadult	Bile acids (subadult)	E	Y	—	—

Species: *Carassius auratus*, goldfish; *Coregonus clupeaformis*, lake whitefish; *Entosphenus tridentatus*, Pacific lamprey; *Ichthyomyzon fossor*, northern brook lamprey; *I. unicuspis*, silver lamprey; *Lampetra appendix*, American brook lamprey; *L. fluviatilis*, river lamprey; *Oncorhynchus kisutch*, coho salmon; *O. mykiss*, rainbow trout; *O. nerka*, sockeye salmon; *Petromyzon marinus*, sea lamprey; *Salmo salar*, Atlantic salmon; *S. trutta*, brown trout; *Salvelinus alpinus*, Arctic char; *S. fontinalis*, brook trout; *S. namaycush*, lake trout.

Methods: BA, behavioural assays; BC, behavioural choice tests; CR, cellular response in olfactory epithelia/bulb; E, electrophysiology; F, field experiments; M, molecular analysis.

Y, yes; N, no.

*Can only determine response, and not attraction, when using methods CR, E and M.

†Specific life stage not known.

may not occur (Keefe & Winn, 1991; Fisknes & Døving, 1982; Quinn, Brannon & Whitman, 1983).

In a field test on the relative importance of pheromones and imprinted cues, Brannon & Quinn (1990) documented the homing behaviour of coho salmon. Adults returned to their juvenile release site rather than a nearby hatchery containing sibling conspecifics, suggesting that imprinted cues are more attractive than population- and family-specific odours. One of the groups in this study, however, returned to a hatchery they had never experienced. These fish had been moved downstream prior to their release as juveniles, which may have disrupted their ability to

imprint on the outmigration route. Their return to the hatchery suggests that conspecific odours can be attractive. These results, taken together with the results from other studies, suggest that conspecific odours may act as a secondary directional cue if imprinting cues are undetectable.

(4) Responses to specific chemical compounds

In addition to exploring the effects of exposure to natal water and conspecifics, many studies have tested the sensitivity of lampreys and salmonids to the component chemicals that contribute to these odours (Table 4). For

Table 4. Sensitivity and attraction to odorants in anadromous fish

Reference	Species	Life-history stage	Odorant	Concentration tested (M)	Detection threshold (M)	Method	Response
Belghaug & Døving (1977)	<i>S. alpinus</i>	Subadult/ adult*	L-Asparagine	—	2.5×10^{-8}	E	
			L-Methionine		6.8×10^{-8}		
			L-Glutamine		6.8×10^{-8}		
			L-Alanine		3.2×10^{-7}		
			L-Homoserine		6.3×10^{-7}		
			L-Serine		9.6×10^{-7}		
			L-Glutamic acid		1.0×10^{-6}		
			L-Leucine		2.10^{-6}		
			L-Histidine		6.8×10^{-6}		
			L-Lysine		6.8×10^{-6}		
			4-Hydroxy-proline		$>10^{-4}$		
			Proline		$>10^{-4}$		
			β -Alanine		$>10^{-4}$		
			Carboxylic acids		$>10^{-4}$		
			Sugars		$>10^{-4}$		
			Taurine		$>10^{-4}$		
			Anserine		6.3×10^{-6}		
Carnosine	$>10^{-5}$						
Glutathione	1.5×10^{-7}						
Phenethyl alcohol	$>10^{-4}$						
Indole	$>10^{-4}$						
Bjerselius <i>et al.</i> (2000)	<i>P. marinus</i>	Migrating adult	Petromyzonal sulfate and cholic acid	5×10^{-6}		BA	Positive
			Petromyzonal sulfate and allocholic acid	5×10^{-10}			
Bodznick (1978b)	<i>O. nerka</i>	Parr	Calcium	5×10^{-10}	5×10^{-6}	E	
			Magnesium		10^{-4}		
			Sodium		$>10^{-3}$		
		Potassium	$>10^{-2}$				
		Calcium	10^{-5} to 10^{-6}		CR		
		Sodium	$>10^{-4}$				
Fry	Calcium	Additional 3.3×10^{-4}	BC	Neutral			
	Calcium	Equivalent to rearing water			Neutral		
Døving <i>et al.</i> (1980)	<i>S. alpinus</i> , <i>T. thymallus</i> (results not distinguished between species)	Subadult/ adult*	Cholic acid		8.0×10^{-8}	E	
			Taurocholic acid		2.0×10^{-8}		
			Taurodeoxycholic acid		6.3×10^{-8}		
			Taurochenodeoxy-cholic acid		4.0×10^{-8}		
			Taurolithocholic acid		6.3×10^{-9}		
			Sulfotaurolithocholic acid		1.0×10^{-8}		
			Methionine		1.3×10^{-6}		
Taurine	1.0×10^{-5}						
Essington & Sorensen (1996)	<i>S. fontinalis</i>	Subadult	Testosterone glucuronide	10^{-7}		E	Positive
			Prostaglandin $F_{2\alpha}$				Positive
			15-keto-PGF $_{2\alpha}$				Positive
			PGF $_{1\alpha}$				Positive
			13,14 Dihydro-15-keto PGF $_{2\alpha}$				Positive
	<i>S. trutta</i>	Subadult	PGF $_{2\alpha}$	10^{-7}			Positive
			15-keto-PGF $_{2\alpha}$				Positive
			PGF $_{1\alpha}$				Positive
			ECG				Positive
	<i>S. fontinalis</i>	Subadult	ECG	10^{-7}			Neutral
	<i>S. trutta</i>	Subadult	13,14 Dihydro-15-keto PGF $_{2\alpha}$	10^{-7}			Neutral
	<i>S. fontinalis</i> , <i>S. trutta</i>	Subadult	Testosterone	10^{-7}			Neutral
			Testosterone-sulphate				Neutral
			Oestradiol				Neutral
DHP			Neutral				

Table 4. Continued

Reference	Species	Life-history stage	Odorant	Concentration tested (M)	Detection threshold (M)	Method	Response	
Evans & Hara (1985)	<i>O. mykiss</i>	Subadult/adult*	17,20 β -P sulphate	10 ⁻⁷	10 ⁻⁹ to 10 ⁻¹⁰ 10 ⁻⁷ to 10 ⁻⁸	PS	Neutral	
			17,20 β -P-glucuronide	10 ⁻⁷			Neutral	
			Prostaglandin E ₂	10 ⁻⁷			Neutral	
			L-Serine					
Fine & Sorensen (2008)	<i>P. marinus</i>	Migrating adult	L-Leucine					
			Petromyzonamine disulfate		10 ⁻¹³	E		
			Petromyzosterol disulfate		10 ⁻¹³	E		
				10 ⁻¹³ , 10 ⁻¹⁴	10 ⁻¹³	BC	Positive	
Fine & Sorensen (2010)	<i>P. marinus</i>	Larvae		10 ⁻¹¹ , 10 ⁻¹²	10 ⁻¹¹	BC	Positive	
			Petromyzonol sulfate		10 ⁻¹²	E		
			Petromyzonamine disulfate		10 ⁻¹¹	BC	Positive	
						MS	Release	
Fine <i>et al.</i> (2004)	<i>P. marinus</i>	Larvae	Petromyzonol sulfate				16 ng larva ⁻¹ h ⁻¹ ; half-life 3 days	
			Petromyzosterol disulfate				Release	
			Petromyzonol sulfate				24 ng larva ⁻¹ h ⁻¹ ; half-life 3 days	
	<i>L. appendix</i>	Larvae	Petromyzonol sulfate				Release	
			Allocholic acid				10 ng larva ⁻¹ h ⁻¹ ; half-life 3 days	
			Petromyzonol sulfate				Release 1.8 ng (g larva) ⁻¹ h ⁻¹	
	<i>I. fossor</i>	Larvae	Petromyzonol sulfate				Release 0.7 ng (g larva) ⁻¹ h ⁻¹	
			Allocholic acid				Release 2.3 ng (g larva) ⁻¹ h ⁻¹	
			Petromyzonol sulfate				Release 0.5 ng (g larva) ⁻¹ h ⁻¹	
	Fisknes & Døving (1982)	<i>S. salar</i>	Subadult/adult*	L-Serine		4 × 10 ⁻⁵	E	Release 1.9 ng (g larva) ⁻¹ h ⁻¹
				L-Glutamine		8 × 10 ⁻⁶		Release 0.8 ng (g larva) ⁻¹ h ⁻¹
	Giaquinto & Hara (2008)	<i>O. mykiss</i>	Adult [†]	Deoxycholic acid		10 ⁻¹⁰	E	
Chenodeoxycholic acid					10 ⁻¹¹			
Cholic acid					10 ⁻¹⁰			
Taurochenodeoxy-cholic acid					10 ⁻¹¹			
Taurocholic acid					10 ⁻¹⁰			
Tauroolithocholic acid					10 ⁻¹¹			
Hara (1972)	<i>O. kisutch</i>	Subadult	L-Serine		10 ⁻⁶ to 10 ⁻⁷	E		
			L-Methionine		10 ⁻⁶ to 10 ⁻⁷			
	<i>O. nerka</i>	Subadult	L-Alanine		10 ⁻⁶ to 10 ⁻⁷			
			L-Serine		>10 ⁻⁶			
Hara (1973)	<i>O. mykiss</i>	Subadult/adult*	L-Methionine		>10 ⁻⁶			
			L-Alanine		>10 ⁻⁶			
Hara (1977)	<i>O. mykiss</i>	Subadult/adult*	L-Serine		10 ⁻⁷ to 10 ⁻⁸	E		
			L-Alanine, L-serine, L-cysteine, L-glutamine	10 ⁻⁴ to 10 ⁻⁵		E	Decreased response when amino group acetylated	
Hara (1977)	<i>O. mykiss</i>	Subadult/adult*	Glycine, L-alanine, L-serine, L-cysteine, L-methionine, L-leucine, L-isoleucine, L-histidine, L-glutamic acid	10 ⁻⁴ to 10 ⁻⁵			Decreased response when alpha-carboxyl group esterified	
			L-Alanine, L-serine, L-leucine	10 ⁻⁴ to 10 ⁻⁵			Decreased response when alpha hydrogen replaced by a methyl group	

Table 4. Continued

Reference	Species	Life-history stage	Odorant	Concentration tested (M)	Detection threshold (M)	Method	Response	
Hara & Zhang (1998)	<i>O. mykiss</i> , <i>S. salar</i> , <i>S. trutta</i> , <i>S. alpinus</i> , <i>S. namaycush</i> , <i>C. clupeiiformis</i>	Adult [†]	Glycine, L-alanine, L-aminobutyric acid, L-norvaline, L-norleucine	10 ⁻⁴ to 10 ⁻⁵			Greatest response in amino acids with three carbon atoms in the chain	
			L-Cysteine		10 ⁻⁹ to 10 ⁻¹⁰	E		
			Taurocholic acid		10 ⁻⁹ to 10 ⁻¹⁰			
Hara <i>et al.</i> (1993)	<i>S. fontinalis</i> , <i>S. alpinus</i> , <i>S. namaycush</i>	Adult [†]	Prostaglandin F _{2α}		10 ⁻¹¹	E		
			15-keto-PGF _{2α}		10 ⁻⁹			
			ECG		10 ⁻¹⁰			
Laberge & Hara (2003)	<i>S. trutta</i>	Adult [†]	L-Cysteine		10 ⁻⁸	BA	Positive	
			L-Serine		10 ⁻⁸			Neutral
			L-Arginine		10 ⁻⁸			
	<i>C. clupeiiformis</i>	Adult [†]	L-Glutamate		10 ⁻⁷	BA	Positive	
			L-Cysteine		10 ⁻⁸			Positive
			L-Serine		10 ⁻⁸			
	<i>O. mykiss</i>	Adult [†]	L-Arginine		10 ⁻⁸	BA	Neutral	
			L-Cysteine		10 ⁻⁹			Neutral
			L-Serine		10 ⁻⁸			
	Laberge & Hara (2004)	<i>O. mykiss</i>	Subadult/ adult*	L-Arginine		10 ⁻⁸	E	
				L-Cysteine		10 ⁻⁸		
				L-Serine		10 ⁻⁸		
Prostaglandin F _{2α}				10 ⁻⁸				
15-keto-PGF _{2α}				10 ⁻⁸				
13,14-Dihydro-PGF _{2α}				10 ⁻⁸				
Prostaglandin F _{2α}				10 ⁻⁸				
15-keto-PGF _{2α}				10 ⁻⁸				
13,14-Dihydro-PGF _{2α}				10 ⁻⁸				
ECG				10 ⁻⁸				
Prostaglandin F _{2α}				10 ⁻⁸				
13,14-Dihydro-PGF _{2α}				10 ⁻⁸				
Prostaglandin F _{1α}	10 ⁻⁸							
15-keto-PGF _{2α}	10 ⁻¹⁰							
15-keto-13,14-dihydro-PGF _{2α}	10 ⁻⁸							
15-keto-PGF _{2α}	10 ⁻⁸							
ECG	10 ⁻⁸							
Prostaglandin F _{2α}	10 ⁻⁶							
ECG	10 ⁻⁷							
Other PGFs	>10 ⁻⁵							
L-Cysteine	10 ⁻⁹							
L-Serine	10 ⁻⁷							
L-Arginine	10 ⁻⁷							
L-Glutamic acid	10 ⁻⁷							

Table 4. Continued

Reference	Species	Life-history stage	Odorant	Concentration tested (M)	Detection threshold (M)	Method	Response
	<i>S. trutta</i>	Subadult/ adult*	L-Cysteine L-Serine L-Arginine L-Glutamic acid L-Cysteine, L-serine, L-arginine, taurocholic acid, PGF _{2α}		10 ⁻⁸ 10 ⁻⁶ 10 ⁻⁶ 10 ⁻⁶	E	Response to bile acids in mid-dorsal region of bulb; to amino acids in latero-posterior region
Li & Sorensen (1997)	<i>P. marinus</i>	Migrating adult	Allocholic acid Cholic acid Deoxycholic acid Petromyzonol Petromyzonol sulfate Lithocholic acid 3-sulfate Glycolithocholic acid 3-sulfate Taurolithocholic acid 3-sulphate Taurocholic acid Taurodeoxycholic acid		10 ⁻¹² 10 ⁻⁹ 10 ⁻⁸ 10 ⁻⁸ 10 ⁻¹² 10 ⁻¹² 10 ⁻¹¹ 10 ⁻¹² 10 ⁻⁸ 10 ⁻⁸	E	
Li <i>et al.</i> (1995)		Migrating adult	Allocholic acid Petromyzonol sulfate Petromyzonol Taurolithocholic acid 3-sulphate		10 ⁻¹² to 10 ⁻¹³ 10 ⁻¹² to 10 ⁻¹³ 10 ⁻⁸ 10 ⁻¹²	E	
Lo <i>et al.</i> (1991)	<i>S. salar</i>	Subadult/ adult*	L-[³ H]alanine L-[³ H]serine	10 ⁻⁷ 10 ⁻⁷		B	
Lo <i>et al.</i> (1994)	<i>S. salar</i>	Subadult/ adult*	Taurocholic acid	10 ⁻⁶ to 10 ⁻⁹		B	
Morin & Døving (1992)	<i>S. salar</i>	Parr	L-Alanine and taurocholate	10 ⁻⁴		E	Even spatial distribution of response to the two chemicals
		Parr-smolt transformation	L-Alanine and taurocholate	10 ⁻⁴			Stronger response to amino acid in lateral region of bulb than in medial
Polkinghorne <i>et al.</i> (2001)	<i>P. marinus</i>	Larvae, adult	Petromyzonol sulfate, allocholic acid, petromyzonol			HPLC	Chemicals produced in liver and gallbladder of larvae, but not in adults
		Larvae	Petromyzonol sulfate Allocholic acid Petromyzonol sulfate, allocholic acid				Released 16 ng larva ⁻¹ h ⁻¹ Released 5 ng larva ⁻¹ h ⁻¹ Released primarily in faeces, half-life of 1 day
Quinn & Hara (1986)	<i>O. kisutch</i>	Parr	L-Arginine L-Cysteine L-Serine Taurocholic acid		10 ⁻⁸ to 10 ⁻⁹ 10 ⁻⁸ to 10 ⁻⁹ 10 ⁻⁸ to 10 ⁻⁹ 10 ⁻⁸ to 10 ⁻⁹	E	
Rehnberg & Schreck (1986)	<i>O. kisutch</i>	Adult*	L-Alanine L-Threonine L-Cysteine Glycine L-Histidine β-Alanine L-Glutamic acid L-Aspartic acid L-Lysine		10 ⁻⁴ 10 ⁻⁴ 10 ⁻⁴ 10 ⁻⁴ 10 ⁻⁴ 10 ⁻⁴ 10 ⁻⁴ 10 ⁻⁴ 10 ⁻⁴	B	
		Parr	L-Threonine L-Serine L-Alanine L-Histidine L-Cysteine β-Alanine L-Aspartic acid Glycine	10 ⁻⁷ 10 ⁻⁷ 10 ⁻⁷ 10 ⁻⁷ 10 ⁻⁷ 10 ⁻⁷ 10 ⁻⁷ 10 ⁻⁷		BC	Avoidance Avoidance Avoidance Avoidance Neutral Neutral Neutral Neutral

Table 4. Continued

Reference	Species	Life-history stage	Odorant	Concentration tested (M)	Detection threshold (M)	Method	Response
		Fry	L-Lysine	10^{-7}		BC	Neutral
			L-Alanine	$35-100 \times 10^{-7}$			Avoidance of L-serine suppressed
			Glycine	$35-100 \times 10^{-7}$			Avoidance of L-serine suppressed
			L-Threonine	$35-100 \times 10^{-7}$			Avoidance of L-serine not suppressed
			L-Aspartic acid	$35-100 \times 10^{-7}$			Avoidance of L-serine not suppressed
			L-Histidine	$35-100 \times 10^{-7}$			Avoidance of L-serine not suppressed
Rehnberg <i>et al.</i> (1985 <i>b</i>)	<i>O. kisutch</i>	Age 0 parr	L-Serine	10^{-6} to 10^{-9}	10^{-8}	BC	Avoidance at $\geq 10^{-8}$ M
		Age 1 parr	L-Serine	10^{-6} to 10^{-8}	10^{-7}		Avoidance at $\geq 10^{-7}$ M
		Smolt (April)	L-Serine	10^{-4} to 10^{-6}	10^{-5}		Avoidance at $\geq 10^{-5}$ M
		Smolt (June)	L-Serine	10^{-6} to 10^{-7}	10^{-6}		Avoidance at $\geq 10^{-6}$ M
		Age 1 parr	L-Alanine	10^{-5} to 10^{-8}	10^{-7}		Avoidance at $\geq 10^{-7}$ M
		Smolt (April)	L-Alanine	10^{-5} to 10^{-7}	10^{-6}		Avoidance at $\geq 10^{-6}$ M
		Smolt (June)	L-Alanine	10^{-5} to 10^{-6}	10^{-5}		Avoidance at $\geq 10^{-5}$ M
Robinson <i>et al.</i> (2009)	<i>E. tridentatus</i>	Migrating adult	Petromyzonol sulfate		10^{-8} to 10^{-9}	E	Significantly less than migrating adults
			3-keto petromyzonal sulfate		10^{-8} to 10^{-9}		
			Allocholic acid		$>10^{-6}$		
			Taurolithocholic acid 3-sulphate		$>10^{-6}$		
		Spawning adult	Petromyzonol sulfate	10^{-6}			
		3-keto petromyzonal sulfate	10^{-6}		Significantly less than migrating adults		
Sato & Suzuki (2001)	<i>O. mykiss</i>	Subadult/adult	L-Alanine, L-arginine, L-glutamic acid, L-norvaline (combined)	10^{-3}		CR	Response in some ciliated olfactory receptor neurons (cORNs) and some microvillous ORNs (mORNs)
			L-Threonine	10^{-3}			Response in some cORNs
			L-Methionine	10^{-3}			
			Glycine	10^{-3}			
			EKG	10^{-4}			
			Taurine	10^{-3}			No response in cORNs or mORNs
			DHP	10^{-4}			
			DHP 20-acetate	10^{-4}			
			DHP 20-sulphate	10^{-4}			
			F-prostaglandin	10^{-4}			
			15-keto-PGF 2α	10^{-4}			
			dPGF	10^{-4}			
			U-46619	10^{-4}			
Satou & Ueda (1975)	<i>O. mykiss</i>	Subadult/adult*	L- α -Alanine		10^{-6} to 10^{-7}	E	Spectral patterns of responses vary among amino acids
			L- α -Alanine		10^{-6} to 10^{-7}		
			L-Serine		10^{-6} to 10^{-7}		
			D-Serine		10^{-6} to 10^{-7}		
			Amino acids	10^{-3}			
Shoji <i>et al.</i> (1996)	<i>O. mykiss</i>	Subadult/adult*	NaCl		10^{-2} to 10^{-3}	E	
			CaCl $_2$		10^{-6} to 10^{-7}		
			MgCl $_2$		10^{-2} to 10^{-3}		
			L-Glutamine		10^{-8}		
			L-Serine		10^{-7}		
			L-Glutamic acid		10^{-7}		
			L-Methionine		10^{-8}		
			L-Alanine		10^{-8}		
			L-Arginine		10^{-8}		

Table 4. Continued

Reference	Species	Life-history stage	Odorant	Concentration tested (M)	Detection threshold (M)	Method	Response
Shoji <i>et al.</i> (2000)	<i>O. masou</i>	Subadult/adult*	Amino acids and salts Inorganic salts Bile acids and salts	HS		E	Positive Neutral Neutral
Shoji <i>et al.</i> (2003)	<i>O. keta</i>	Spawning adult	Amino acids, taurine, urea and ammonia	HS		BC	Positive
Shparkovskiy <i>et al.</i> (1981)	<i>O. gorbuscha</i>	Spawning adult	Amino acids (mixture)	10 ⁻⁵		BA	Positive
			D,L-Valine	10 ⁻⁵			Neutral
			L-Cysteine	10 ⁻⁵			Neutral
			L-Glutamine	10 ⁻⁵			Positive
			D,L-Asparagine	10 ⁻⁵			Positive
			D,L-Serine	10 ⁻⁵			Positive
			D,L-Leucine	10 ⁻⁵			Positive
			L-Arginine	10 ⁻⁵			Neutral
			D,L-Alanine	10 ⁻⁵			Negative
			L-Cystine	10 ⁻⁵			Neutral
			L-Lysine	10 ⁻⁵			Neutral
			L-Arabinose	10 ⁻⁴			Neutral
			Sucrose	10 ⁻⁴			Neutral
			D-Lactose	10 ⁻⁴			Neutral
			D-Mannitol	10 ⁻⁴			Neutral
			D-Glucose	10 ⁻⁴			Neutral
			D-Maltose	10 ⁻⁴			Neutral
	<i>S. salar</i>	Spawning adult	Amino acids (mixture)	10 ⁻⁵		BA	Positive
			D,L-Valine	10 ⁻⁵			Negative
			L-Cysteine	10 ⁻⁵			Positive
			L-Glutamine	10 ⁻⁵			Positive
			D,L-Asparagine	10 ⁻⁵			Positive
			D,L-Serine	10 ⁻⁵			Neutral
			D,L-Leucine	10 ⁻⁵			Positive
			L-Arginine	10 ⁻⁵			Neutral
			D,L-Alanine	10 ⁻⁵			Negative
			L-Cystine	10 ⁻⁵			Neutral
			L-Lysine	10 ⁻⁵			Neutral
			L-Arabinose	10 ⁻⁴			Neutral
			Sucrose	10 ⁻⁴			Neutral
			D-Lactose	10 ⁻⁴			Neutral
			D-Mannitol	10 ⁻⁴			Neutral
			D-Glucose	10 ⁻⁴			Neutral
			L-Maltose	10 ⁻⁴			Neutral
Shparkovskiy, Pavlov & Chinarina (1983)	<i>S. salar</i>	Zero age parr, 1 year parr, Immature adult	Amino acids (mixture)	10 ⁻⁴		BA	Positive
			L-Alanine	10 ⁻⁴			Neutral
			D,L-Arginine	10 ⁻⁴			Negative
			L-Aspartic acid	10 ⁻⁴			Positive
			D,L-Valine	10 ⁻⁴			Positive
			Histidine	10 ⁻⁴			Negative
			L-Glutamic acid	10 ⁻⁴			Positive
			L-Leucine	10 ⁻⁴			Positive
			L-Lysine	10 ⁻⁴			Neutral
			D,L-Methionine	10 ⁻⁴			Neutral
			D,L-Serine	10 ⁻⁴			Neutral
			Threonine	10 ⁻⁴			Neutral
			D,L-Tryptophan	10 ⁻⁴			Neutral
			L-Cysteine	10 ⁻⁴			Neutral
			L-Cystine	10 ⁻⁴			Neutral
Siefkes & Li (2004)	<i>P. marinus</i>	Migrating adult	3-keto petromyzonal sulfate		10 ⁻¹²	E	
			3-keto allocholic acid		10 ⁻¹⁰		
			Petromyzonal sulfate		10 ⁻¹⁰		
			Allocholic acid		10 ⁻¹⁰		
Sorensen <i>et al.</i> (2005)	<i>P. marinus</i>	Migrating adult	Petromyzonamine disulfate	10 ⁻¹² to 10 ⁻¹⁴	10 ⁻¹³	E	
			Petromyzosterol disulfate		10 ⁻¹³	BC	Positive at $\geq 10^{-13}$ M
					10 ⁻¹³	E	

Table 4. Continued

Reference	Species	Life-history stage	Odorant	Concentration tested (M)	Detection threshold (M)	Method	Response
				10^{-11} to 10^{-12}	10^{-11}	BC	Positive at 10^{-11} M
			Petromyzonol sulfate	10^{-11} to 10^{-12}	10^{-12}	E	
					10^{-11}	BC	Positive at 10^{-11} M
Sutterlin & Sutterlin (1971)	<i>S. salar</i>	Smolt	L-Alanine		3.2×10^{-9}	E	
			L-Threonine		2.5×10^{-6}		
			L-Proline		3.2×10^{-5}		
			Various carboxylic acids, sugars, alcohols, amines				No response
Sveinsson & Hara (1990a)	<i>S. alpinus</i>	Not given	L-Cysteine		$<10^{-9}$	E	
Sveinsson & Hara (1990b)	<i>S. alpinus</i>	Not given	L-Arginine		$<10^{-8}$	E	
			L-Histidine		$<10^{-7}$		
			L-Alanine		$<10^{-7}$		
			L-Cysteine		$<10^{-9}$		
Sveinsson & Hara (2000)	<i>S. alpinus</i>	Subadult or early-stage mature adult	Prostaglandin $F_{2\alpha}$		10^{-10} to 10^{-12}	E	
			5- <i>trans</i> -PGF $_{2\alpha}$		10^{-9} to 10^{-10}		
			16-Phenyl-tetranor-PGF $_{2\alpha}$		10^{-10}		
			11 β -PGF $_{2\alpha}$		10^{-8} to 10^{-9}		
			16,16-Dimethyl-PGF $_{2\alpha}$		10^{-10} to 10^{-12}		
			U-46619		10^{-10} to 10^{-12}		
			15-keto-PGF $_{2\alpha}$		$>10^{-8}$		
			15(R)-PGF $_{2\alpha}$		$>10^{-8}$		
			I-BOP		10^{-9}		
			Prostaglandin $F_{1\alpha}$		10^{-9} to 10^{-10}		
			13,14-Dihydro-PGF $_{1\alpha}$		10^{-9} to 10^{-10}		
			PGF $_{3\alpha}$		10^{-9} to 10^{-10}		
			PGF $_{2\beta}$		10^{-9} to 10^{-10}		
Vrieze & Sorensen (2001)	<i>P. marinus</i>	Migrating adult	Petromyzonal sulfate	10^{-10}		BC	Neutral
Yamamoto & Ueda (2009)	<i>O. keta</i>	Spawning adult	Allocholic acid	0.15×10^{-10}		BC	Neutral
			Amino acids and related substances	HS			Positive
			Amino acids excluding L-glutamic acid				Positive
			Amino acids and related substances			E	Positive
			Amino acids excluding L-glutamic acid				Positive
Yamamoto <i>et al.</i> (2008a)	<i>O. gorbuscha</i>	Spawning adult	Amino acids	HS		BC	Positive/neutral (no statistical tests)
	<i>O. keta</i>	Spawning adult	Amino acids			BC	Positive (no statistical tests)
	<i>O. masou</i>	Spawning adult	Amino acids			BC	Positive (no statistical tests)
	<i>O. nerka</i>	Spawning adult	Amino acids			BC	Positive (no statistical tests)
Yamamoto <i>et al.</i> (2008b)	<i>O. mykiss</i>	Parr	L-Alanine		10^{-7}	E	
Yamamoto <i>et al.</i> (2013)	<i>O. keta</i>	Spawning adult	Amino acids	HS (during outmigration)		BC	Positive
			Amino acids	HS (spawning migration)		E	Positive
						BC	Positive
						E	Positive

Table 4. Continued

Reference	Species	Life-history stage	Odorant	Concentration tested (M)	Detection threshold (M)	Method	Response				
Yun <i>et al.</i> (2011)	<i>L. tridentata</i>	Migrating adult	Petromyzonamine disulfate		10^{-14}	E					
			Petromyzosterol disulfate		10^{-13}						
			Petromyzonal sulfate		10^{-14}						
			3-keto petromyzonal sulfate		10^{-14}						
			Allocholic acid		10^{-9}						
Yun <i>et al.</i> (2003)	<i>L. tridentata</i>	Larvae	3-keto allocholic acid		10^{-10}	HPLC	Release 1.48 ng (g larva) ⁻¹ h ⁻¹				
	<i>L. richardsonii</i>	Larvae	Petromyzonal sulfate				Released 30.68 ng (g larva) ⁻¹ h ⁻¹				
	<i>P. marinus</i>	Larvae	Petromyzonal sulfate				Released 36.77 ng (g larva) ⁻¹ h ⁻¹				
Zhang <i>et al.</i> (2001)	<i>S. namaycush</i>	Subadult	Taurocholic acid			HPLC	Release 268.5 ± 5.1 nmol μl ⁻¹ in bile, 23.4 ± 0.7 nmol mg ⁻¹ in feces, 2.6 ± 2.4 nmol h ⁻¹ in urine, 2.8 ± 1.1 nmol min ⁻¹ kg ⁻¹ in water				
			Taurochenodeoxy-cholic acid				Release 15.0 ± 0.8 nmol μl ⁻¹ in bile, 3.1 ± 0.3 nmol mg ⁻¹ in faeces, 1.4 ± 1.4 nmol h ⁻¹ in urine, 0.9 ± 0.2 nmol min ⁻¹ kg ⁻¹ in water				
			Taurolithocholic acid				Release 0.1 ± 0.1 nmol μl ⁻¹ , trace in faeces, none in urine or water				
			Taurooxocholanic acid				Release 20.5 ± 0.0 nmol μl ⁻¹ in bile, 3.5 ± 0.7 nmol mg ⁻¹ in faeces, none in water				
			Tauroxodeoxycholic acid 3α-sulphate				Release 7.8 ± 0.2 nmol μl ⁻¹ in bile, 1.3 ± 0.1 nmol mg ⁻¹ in feces, 0.2 ± 0.2 nmol h ⁻¹ in urine, trace in water				
			Taurocholic acid		10^{-9} to 10^{-10}		E				
			Taurochenodeoxy-cholic acid		10^{-9} to 10^{-10}						
			Zhang & Hara (2009)	<i>S. namaycush</i>	Subadult/ adult*		Sulphated fractions		10^{-9}	E	
							CD		2×10^{-11}		
							DA		2×10^{-9}		
3-Dehydrocholic acid		2×10^{-11}									
Cholic acid		10^{-10}									
Hyochoic acid		2×10^{-10}									
7-Oxo-DA		10^{-9}									
12-Oxo-CD		2×10^{-9}									
3-Deoxycholic acid		2×10^{-11}									
Isodeoxycholic acid		5×10^{-9}									
Allocholic acid		10^{-8}									
Lithocholic acid		10^{-8}									
Petromyzonol		2×10^{-8}									
5β-Petromyzonol		2×10^{-8}									
Dehydrocholic acid		2×10^{-7}									
Nordeoxycholic acid		2×10^{-7}									
Cholanic acid		2×10^{-7}									
5β-Epicholestanol		2×10^{-6}									
Taurochenocholic acid		5×10^{-10}									
Taurocholic acid		5×10^{-10}									

Table 4. Continued

Reference	Species	Life-history stage	Odorant	Concentration tested (M)	Detection threshold (M)	Method	Response
			Tauro-DA		2×10^{-9}		
			Glycocholic acid		10^{-8}		
			Glycocheno-DA		2×10^{-8}		
			Taurolithocholic acid		2×10^{-8}		
			Glyco-DA		5×10^{-8}		
			Taurohyo-DA		10^{-7}		
			Taurourso-DA		10^{-7}		
			Glycolithocholic acid		5×10^{-7}		
			Taurodehydrocholic acid		5×10^{-7}		
			Taurocholanic acid		10^{-6}		
			CD diacetate methyl ester		10^{-6}		
			Taurolithocholic acid 3 α -sulphate		2×10^{-11}		
			Taurocholic acid 3 α ,7 α ,12 α -trisulphate		10^{-10}		
			Petromyzonol sulphate		10^{-9}		
			Lithocholic acid 3 α -S		2×10^{-9}		
			Glycolithocholic acid 3 α -sulfate		5×10^{-9}		
			Deoxycholic acid 3 α ,12 α -sulphates		5×10^{-8}		
			Ursodeoxycholic acid 3 α ,7 β -disulphate		10^{-7}		
			Cholic acid 3 α ,7 α ,12 α -trisulphate		2×10^{-7}		
			Prostaglandin F2 α		10^{-12}		
			L-Cysteine		10		
			DHP		>10		

Species: *Coregonus clupeaformis*, lake whitefish; *Entosphenus tridentatus*, Pacific lamprey; *Ichthyomyzon fossor*, northern brook lamprey; *Lampetra richardsonii*, western brook lamprey; *Lethenteron appendix*, American brook lamprey; *Oncorhynchus gorbusha*, pink salmon; *O. keta*, chum salmon; *O. kisutch*, coho salmon; *O. masou*, masu salmon; *O. mykiss*, steelhead/rainbow trout; *O. nerka*, sockeye salmon; *Petromyzon marinus*, sea lamprey; *Salmo salar*, Atlantic salmon; *S. trutta*, brown trout; *Salvelinus alpinus*, Arctic char; *S. fontinalis*, brook trout; *S. namaycush*, lake trout; *Thymallus thymallus*, grayling.

Odorants: CD, chenodeoxycholic acid; DA, deoxycholic acid; DHP, 17 α ,20 β -dihydroxy-4-pregnene-3-one; ECG, etiocholam-3 α -ol-17-one glucuronide; I-BOP, 7-[3-[3-hydroxy-4-(4-iodophenoxy)-butenyl]-7-oxabicycloheptyl]-5-heptanoic acid; PG, prostaglandin; U-46619, 9,11-dideoxy-9 α ,11 α -methanoepoxy prostaglandin F_{2 α} .

Concentration tested: HS, chemicals tested at the concentration present in the homestream.

Methods: B, binding of olfactory receptors; BA, behavioural assays; BC, behavioural choice tests; CR, cellular response in olfactory epithelia/bulb; E, electrophysiology; HPLC, high-performance liquid chromatography; MS, mass spectrometry; PS, phospholipid staining.

*Specific life-history stage not given.

†Have reached maturity, but reared in captivity (and therefore not classified as either 'migrating adult' or 'spawning adult').

migratory lamprey species, several bile acids have been identified as potent chemical cues that direct adults towards spawning grounds (Li, Sorensen & Gallaher, 1995; Li & Sorensen, 1997; Vrieze & Sorensen, 2001; Fine *et al.*, 2004; Siefkes & Li, 2004; Sorensen *et al.*, 2005; Robinson *et al.*, 2009; Yun *et al.*, 2011). These chemicals are released by larval lamprey, primarily through their faeces, at levels detectable by migrating adults (Polkinghorne *et al.*, 2001; Fine *et al.*, 2004; Fine & Sorensen, 2010). When isolated, the chemicals can trigger an attractive response similar to that of larval water (Sorensen *et al.*, 2005; Fine & Sorensen, 2008).

In salmonids, however, the directional cues have not yet been identified. Four classes of chemicals are detected at very low concentrations by the fish olfactory system. Amino acids and some steroids are detected

at the micromolar to nanomolar range, while bile acids and bile salts are detected at the nanomolar to picomolar range, and prostaglandins are detected at the micromolar to picomolar range (Table 4). Salmonids can also detect cations (such as calcium and magnesium) at millimolar to micromolar levels (Bodznick, 1978b; Shoji *et al.*, 1996). The detection thresholds for each of these classes of chemicals are within their range of concentrations in natural freshwater systems, and they are therefore all potential migratory cues (Zielinski & Hara, 2007).

Salmonids and lampreys detect aquatic odorants through complex signal transduction mechanisms. Separate receptors exist for different classes of chemicals, such as amino acids, prostaglandins, bile acids and salts, and other steroids (Døving, Selset & Thommesen, 1980;

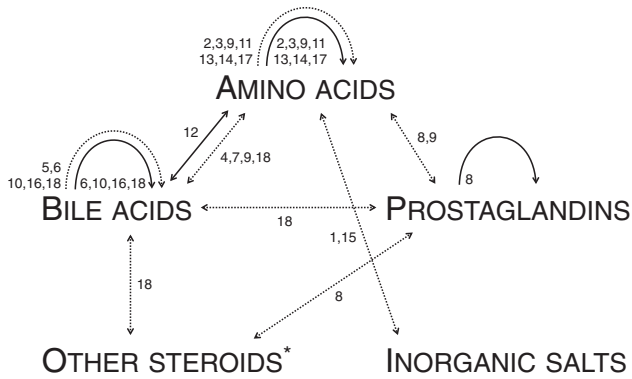


Fig. 2. Interactions between different classes of chemicals in the olfactory system of anadromous fish. Solid lines indicate suppression, and therefore shared transduction mechanisms and/or olfactory receptors. Dashed lines indicate no suppression, and therefore different transduction mechanisms and/or olfactory receptors (signifying the ability to discriminate). *ECG, etiocholam-3 α -ol-17-one glucuronide; DHP, 17 α ,20 β -dihydroxy-4-pregnene-3-one. 1, Bodznick (1978b); 2, Brown & Hara (1981); 3, Cagan & Zieger (1978); 4, Døving *et al.* (1980); 5, Fine & Sorensen (2008); 6, Giaquinto & Hara (2008); 7, Hara & Zhang (1998); 8, Laberge & Hara (2003); 9, Laberge & Hara (2004); 10, Li & Sorensen (1997); 11, Lo *et al.* (1991); 12, Lo *et al.* (1994); 13, MacLeod (1976); 14, Rehnberg & Schreck (1986); 15, Shoji *et al.* (1996); 16, Siefkes & Li (2004); 17, Sveinsson & Hara (1990b); 18, Zhang & Hara (2009).

Laberge & Hara, 2004; Zhang & Hara, 2009), allowing the fish to discriminate between the different classes. Furthermore, amino acids, bile acids, and prostaglandins can suppress responses to other chemical compounds within their class (Rehnberg & Schreck, 1986; Lo, Bradley & Rhoads, 1991; Laberge & Hara, 2003, 2004; Giaquinto & Hara, 2008), indicating that certain receptors are able to bind multiple chemicals within a given class. There is also evidence, however, that different receptor types exist for certain chemical classes. There appear to be different types of receptors for amino acids (Sveinsson & Hara, 1990b) as well as for bile acids (Siefkes & Li, 2004; Fine & Sorensen, 2008; Zhang & Hara, 2009), allowing for discrimination between, for example, free bile acids and amidated bile acids, or neutral and basic amino acids. Prostaglandins, meanwhile, may activate as few as a single receptor type (Laberge & Hara, 2003). Reception of different chemical classes also triggers a response in different regions of the olfactory bulb (Døving *et al.*, 1980; Fisknes & Døving, 1982; Morin & Døving, 1992; Hara & Zhang, 1998; Laberge & Hara, 2004). Taken together, this information suggests that the fish can discriminate among, and also within, different groups of chemical compounds (Fig. 2).

Recently, amino acids have been identified as a primary candidate for migratory cues in salmonids. Shoji

et al. (2000) created three types of artificial natal water by adding the appropriate concentrations of certain groups of chemicals to blank water, thus replicating the concentrations found in the natal water. The three separate artificial 'natal waters' contained: (i) amino acids and inorganic salts; (ii) bile acids and inorganic salts; or (iii) inorganic salts alone. The electrophysiological response of mature masu salmon (*Oncorhynchus masou*) to the amino acid mixture was similar in strength to their response to the true natal water, whereas the response to the other artificial waters was substantially lower. Shoji *et al.* (2003) used behavioural choice tests to demonstrate that chum salmon (*O. keta*) are attracted to artificial natal water containing the appropriate concentrations of amino acids, taurine, urea, and ammonia, and Yamamoto, Ishizawa & Ueda (2008a) produced similar results with sockeye salmon (*O. nerka*), masu salmon and pink salmon (*O. gorbuscha*). Furthermore, Yamamoto & Ueda (2009) determined that chum salmon are attracted to artificial natal water containing only amino acids and salts, even when the amino acid that is most abundant in their natal stream is removed.

(5) Olfactory imprinting

Olfactory imprinting, which is the most widely accepted explanation of natal homing in salmonids, has been tested extensively (Table 5). While the specific natural chemicals that are imprinted on have not yet been identified, artificial imprinting studies have convincingly demonstrated the imprinting abilities of salmonids. After being exposed as juveniles to a chemical that is absent from natural water systems, such as morpholine or phenethyl alcohol, adults become sensitive and attracted to that chemical. This has been demonstrated in various salmonid species, including coho salmon (*Oncorhynchus kisutch*; Cooper *et al.*, 1976; Scholz *et al.*, 1976; Rehnberg, Curtis & Schreck, 1985a), Chinook salmon (*O. tshawytscha*; Hassler & Kutchins, 1990), sockeye salmon (*O. nerka*; Tilson & Scholz, 1997), steelhead (*O. mykiss*; Cooper & Scholz, 1976), and brown trout (*Salmo trutta*; Scholz *et al.*, 1978a).

Field studies indicate that coho salmon can successfully imprint in as few as 2 days (Jensen & Duncan, 1971), while successful imprinting has been demonstrated in as few as 14 days in a laboratory study (Yamamoto, Hino & Ueda, 2010). The precise moment at which imprinting occurs, however, has not been conclusively identified. Most studies on the timing of olfactory imprinting indicate that the parr-smolt transformation (PST) is a critical period. Thyroid hormones, which have been linked to memory development (Morin, Dodson & Doré, 1989a,b; Nevitt *et al.*, 1994), undergo a marked increase during this period of growth (Dickhoff, Folmar & Gorbman, 1978), which may explain why the PST is a sensitive imprinting period. In some species of salmonids, however, juveniles migrate to a nursery lake or river before undergoing the

Table 5. Studies exploring the timing of imprinting in salmonids

Reference	Species	Life stages imprinted	Imprinting chemical	Concentration	Duration of exposure	Method	Life stage of successful imprinting	Notes
Cooper & Scholz (1976)	<i>O. mykiss</i>	PST	Morpholine	10^{-10}	1 month	F	PST	—
Cooper & Hasler (1974)	<i>O. kisutch</i>	PST	Morpholine	10^{-10}	5 weeks	E	PST	—
Cooper <i>et al.</i> (1976)	<i>O. kisutch</i>	PST	Morpholine	10^{-7} to 10^{-10}	5–7 weeks	F	PST	Also tested reduced exposure duration (2 days) and monitored returns to decoy stream 1 year early. Increased number of jacks returning
Dittman <i>et al.</i> (1996)	<i>O. kisutch</i>	Alevin, parr, smolt	PEA	10^{-7}	1.5–3 weeks	BC	Smolt	—
Dittman <i>et al.</i> (1997)	<i>O. kisutch</i>	Embryo-fry, parr, smolt	Hatchery water	—	1.5–9 weeks	F	Inconclusive	—
Dittman <i>et al.</i> (1997)	<i>O. kisutch</i>	PST	PEA	10^{-7}	10 days	BC	PST	Olfactory cilia guanylyl cyclase sensitized to imprinted odorant in mature adults
Dukes <i>et al.</i> (2004)	<i>S. salar</i>	—	—	—	—	G	PST	Increased expression during PST
Hara & Brown (1979)	<i>O. mykiss</i>	Parr, PST, smolt	Morpholine	5.7×10^{-10}	5 months	E	None	No increase in response up to 12 months after exposure (did not test mature adults)
Hassler & Kutchins (1990)	<i>O. ishawytscha</i>	PST	Morpholine	10^{-10}	17–40 days	F	None	—
Johnsen & Hasler (1980)	<i>O. kisutch</i>	PST	Morpholine	10^{-10}	1 month	F	PST	—
Lema & Nevitt (2004)	<i>O. kisutch</i>	—	—	—	—	CP	PST	Positive relationship between thyroxine and cellular proliferation during smoltification
Morin & Døving (1992)	<i>S. salar</i>	Parr, PST, smolt	Taurocholate or L-alanine	10^{-7}	0–10 weeks	E	—	Peak response during PST
Morin <i>et al.</i> (1989 <i>a,b</i>)	<i>S. salar</i>	PST	L-Cysteine	3.8×10^{-4}	—	CC	—	Strongest response during mid-point of smoltification (21–28 days after onset), suggesting this is key imprinting period
Morin, Hara & Eales (1995)	<i>S. salar</i>	—	L-Alanine	10^{-5} to 10^{-9}	—	E	—	Artificially increasing plasma L-thyroxine (to mimic the natural increase during smoltification) reduced olfactory sensitivity
Morin, Hara & Eales (1997)	<i>S. salar</i>	—	L-Alanine	10^{-5} to 10^{-9}	—	E	—	Plasma L-thyroxine surged during middle of PST, but no change in electrophysiological response

Table 5. Continued

Reference	Species	Life stages imprinted	Imprinting chemical	Concentration	Duration of exposure	Method	Life stage of successful imprinting	Notes
Nevitt <i>et al.</i> (1994)	<i>O. kisutch</i>	PST	PEA	10^{-7}	10 days	BC, CR	PST	Results suggest imprinting memory stored in the peripheral nervous system
Rehnberg <i>et al.</i> (1985a)	<i>O. kisutch</i>	Smolt	Morpholine	10^{-10}	15 days	F	Inconclusive	Released morpholine in their natal water. Control (unexposed) salmon returned in equal numbers to exposed salmon
Rehnberg <i>et al.</i> (1985b)	<i>O. nerka</i>	—	L-Serine, D,L-alanine	—	—	BC	—	Threshold concentration for avoidance response higher during PST and postPST than in parr, suggesting potentially reduced sensitivity
Sahafi (2013)	<i>R. frisii</i>	Yolk sack, active fry, fingerling	Morpholine	10^{-7} to 10^{-12}	Not given	F	Active fry	Very small sample size (two control adults returned, 4–14 adults returned in treatment groups)
Scholz <i>et al.</i> (1976)	<i>O. kisutch</i>	PST	Morpholine/PEA	10^{-10} (M), 8×10^{-9} (PEA)	1.5 months	F	PST	—
Scholz <i>et al.</i> (1978a)	<i>S. trutta</i>	PST	Morpholine	10^{-10}	34 days	F	PST	—
Scholz <i>et al.</i> (1978b)	<i>O. mykiss</i>	PST	Morpholine	10^{-10}	73 days	F	PST	—
Shimizu <i>et al.</i> (1995)	<i>O. masou</i>	—	—	—	—	—	—	Various unknown proteins in the olfactory system appeared or disappeared during smoltification
Yamamoto <i>et al.</i> (2010)	<i>O. nerka</i>	Parr, PST, smolt	L-Proline	10^{-6}	1, 6 h; 1, 7, 14 days	E	Parr, PST	Successful imprinting following 14 days of exposure, but not other exposure durations
		Parr, PST, smolt	L-Proline	10^{-6}	1, 6 h; 1, 7, 14 days	BC	Parr, PST	—

Species: *Oncorhynchus kisutch*, coho salmon; *O. masou*, masu salmon; *O. mykiss*, steelhead/rainbow trout; *O. nerka*, sockeye salmon; *O. tshawytscha*, Chinook salmon; Atlantic salmon; *S. trutta*, brown trout; *Rutilus frisii*, kutum.

Method: BC, behavioural choice; CC, cardiac conditioning; CR, cellular proliferation; CR, cellular response; E, electrophysiology; F, field experiment (imprinting chemical released into decoy stream and adult returns monitored); G, olfactory receptor gene expression.

PEA, phenethyl alcohol; PST, parr–smolt transformation.

PST. This implies that imprinting should occur prior to the PST, although experimental evidence of pre-PST imprinting is limited (Tilson & Scholz, 1997). Dittman & Quinn (1996) propose that the lack of evidence of imprinting before the PST may be due to a lack of environmental variability in imprinting studies. Juveniles in such studies are often reared in a hatchery environment (Hasler & Scholz, 1983; Dittman, Quinn & Nevitt, 1996; Dittman *et al.*, 1997), where rearing conditions remain static (i.e. the fish are held in the same water throughout development). Static rearing conditions could limit imprinting to the developmentally controlled surge in thyroid hormones during the PST. In addition to developmentally controlled peaks of thyroid hormone levels, however, the thyroid axis is affected by exposure to novel water (Dickhoff *et al.*, 1978; Hoffnagle & Fivizzani, 1990) and other environmental cues (Dittman & Quinn, 1996). Since hatchery fish remain in the same water, they do not experience an increase in thyroid levels that is associated with exposure to novel water. This may, at least in part, explain why experimental fish have historically been unable to imprint before the PST.

Large-scale field studies, in which the juvenile outmigration of salmonids is altered, also provide valuable insight into the imprinting process of juveniles. Juveniles that are reared in one location and released in another, typically during or close to the PST, tend to return to the site of release (Table 6). These results underline that the PST is a sensitive period for imprinting. Furthermore, juveniles that are released closer to their rearing site often return to the rearing site (e.g. Brannon & Quinn, 1990; Nordeng & Bratland, 2006), unlike those released further away (e.g. Donaldson & Allen, 1958; Jensen & Duncan, 1971; Johnson, Solazzi & Nickelson, 1990), which may indicate that juveniles imprint to multiple waypoints, as proposed by Harden Jones (1968). In other words, as adults return, they may first locate the release site, then make their way onwards to the rearing site if it is within detection range.

(6) Molecular ecology of olfaction during the spawning migration

Although the majority of studies to date have focused on the behaviour, physiology, and ecology of olfactory imprinting, recent genetic research has improved our understanding of the olfactory system in salmonids from a molecular standpoint. Various olfactory genes have been characterized in salmonids, particularly in Atlantic salmon (*Salmo salar*; Wickens, May & Rand-Weaver, 2001; Dukes *et al.*, 2006; Johnstone *et al.*, 2009, 2012), but also in several species of Pacific salmon and trout (*Oncorhynchus* spp.; Onuma *et al.*, 2005; Hino *et al.*, 2007; Kudo *et al.*, 2009; Johnson & Banks, 2011), and most recently in sea lamprey (*Petromyzon marinus*; Chang, 2013). Much of the research in these fish has focused on olfactory receptor genes, which encode for receptors in the olfactory epithelia. In teleosts, which

lack a vomeronasal organ, these genes can be classified into four families: trace amine-associated receptors, vomeronasal family 1-like receptors, vomeronasal family 2-like receptors, and main olfactory receptors (Johnstone *et al.*, 2012). These genes are highly conserved across various species (Morinishi *et al.*, 2007; Johnson & Banks, 2011), signifying their importance to the life history of salmonids. Also, the expression of olfactory genes is dynamic, changing over time and across life stages (Dukes *et al.*, 2004; Johnstone *et al.*, 2011), with an increase in expression, for example, during the PST (Dukes *et al.*, 2004; Yamamoto *et al.*, 2010).

IV. GAPS IN OLFACTION AND SPAWNING MIGRATION RESEARCH

Based on our review of the research to date, we identified several research gaps that warrant further exploration.

(1) Species- and population-level differences

Salmonids vary in their homing abilities across species, and this may be related to evolutionary differences. Ueda (2011), for example, suggests that species-level differences in homestream fidelity among Pacific salmon (*Oncorhynchus* spp.) may reflect their evolutionary history. Pink salmon (*O. gorbuscha*) exhibit the lowest level of homestream fidelity (Heard, 1991), which may enable rapid colonization of new habitat (Pess *et al.*, 2012). There is evidence that pink salmon are the most derived species of Pacific salmon (Murata *et al.*, 1996), and Ueda (2011) suggests they may have evolved a less precise form of homing that has allowed them to become the most widely distributed species in their genus.

Ecological and life-history factors may also influence homestream fidelity. Extended freshwater experience might increase fidelity, as evidenced by a paired-release study by Westley, Quinn & Dittman (2013) that found greater homing success in stream-type Chinook salmon (*O. tshawytscha*) than ocean-type Chinook. Quinn (1984) hypothesized that fidelity is also higher in stable streams, because there is less risk of mortality due to a natural disaster. He also hypothesized that variation in age at maturity could reduce a population's susceptibility to a natural disaster, and therefore increase homestream fidelity. This latter factor might suggest that, although both species migrate to the ocean within their first year, chum salmon (*O. keta*) have greater homestream fidelity than pink salmon, since chum salmon vary in their age at maturity, whereas pink salmon do not. Also, the proximity of suitable habitat in relation to the natal site may influence fidelity, as the frequency of straying decreases with increasing distance from the homestream (Keefer & Caudill, 2014).

Table 6. Studies in which juvenile salmonids were transplanted before or during their outmigration, and adult returns were monitored

Reference	Species	Age at trans- port	Transport location	Distance (km)	Number released	Number returns	% to release site	% to rearing site	% to other sites	Imprinted site	Notes
Brannon & Quinn (1990)	<i>O. kisutch</i>	Fry	Within lake	10	19637	82	100	0	—	Release	—
Donaldson & Allen (1958)	<i>O. kisutch</i>	Smolt	Within lake	10	10020	38	84	16	—	Release	—
	<i>O. kisutch</i>	PST	Adjacent river	75	34405	124	100	0	—	Release	—
	<i>O. tshawytscha</i>	PST	Adjacent river	150	36833	70	100	0	—	Release	—
Ebel, Park & Johnsen (1973)	<i>O. tshawytscha</i>	Smolt	Downstream	200 or 300	131958	—	—	—	—	—	Increased returns to rearing site when transported downstream (relative to controls)
Foster & Schom (1989)	<i>O. mykiss</i>	Kelt	Different river system	150	72647	5	0	100	—	—	Delayed release of nine other kelts, but none recovered
	<i>S. salar</i>										
Hansen & Jonsson (1994)	<i>S. salar</i>	Smolt	Different river system	Not given	847	27	85	≥ 15	≥ 15	Release	Returns to rearing site and other rivers not distinguished
Jensen & Duncan (1971)	<i>O. kisutch</i>	Smolt	Downstream	260	650000	1712	100	0	—	Release	—
Johnson <i>et al.</i> (1990)	<i>O. kisutch</i>	Smolt	Different river system	177	398265	2307*	99.9	0.1	—	Release	*Based on recovery estimates
Keefer <i>et al.</i> (2008b)	<i>O. tshawytscha</i>	Smolt	Downstream	11	208100	—	—	121 *	—	—	*Not possible to estimate percentages based on data collected
		None	Upstream	23	208048	—	—	720 *	—	—	Smolts barged downstream, but water from river circulated continuously
	Smolt	Downstream	>350	—	245	—	—	82.5	17.6	—	
	None	NA	NA	NA	—	161	—	92.6	7.4	—	
	Smolt	Downstream	>350	—	409	—	—	75.6	24.4	—	
McIsaac & Quinn (1988)	None	None	NA	NA	—	238	—	88.7	11.3	—	
	Eggs	Downstream	Downstream	370	—	894	—	58	42	—	Rearred from hatching until release at same site
Nordeng (1971)	<i>S. alpinus</i>	Smolt	Estuary	~1500	174	31	32	—	68	—	Rearred in different river system, released 10 km from estuary of ancestral river. 'Other sites' = ancestral river
Nordeng (2009)	<i>S. alpinus</i>	Smolt	Estuary	~1500	143	27	96	—	4	—	Rearred in different river system, released at estuary of ancestral river. 'Release site' = ancestral river
		Smolt	Coastal ocean	~1500	291	63	—	65	35	—	—
Nordeng & Bratland (2006)	<i>S. alpinus</i>	Smolt	Different river system	8	188	66	9	88	3	Rearing	—

Table 6. Continued

Reference	Species	Age at trans-port	Transport location	Distance (km)	Number released	Number returns	% to release site	% to rearing site	% to other sites	Imprinted site	Notes
			Coastal ocean	8, then 10	43	17	6	88	6	Rearing	Held 3 days in different river then released in ocean
	<i>S. trutta</i>	Smolt	Different river system	8	109	14	0	100	0	Rearing	—
			Coastal ocean	8, then 4	80	24	4	96	0	Rearing	Held 3 days in different river then released in ocean
Quinn <i>et al.</i> (1989)	<i>O. kisutch</i>	Smolt	Downstream	18	10020	51	86	14	—	Release	Held at rearing site until fully completed PST
		Smolt	Downstream	4	8491	34	—	100 *	0	Rearing	*Hatchery site
		Smolt	Downstream	40	10000	17	88	12	—	Release	Held at rearing site until fully completed PST
Savitz, Bardygula & Funk (1993)	<i>O. kisutch</i>	Parr	Lake Michigan	Un-known	50436	8	63	—	38	—	'Other sites' are other harbours in Lake Michigan
		Smolt	—	—	50427	19	84	—	16	—	—
	<i>O. tshawytscha</i>	Parr	—	—	148937	52	52	—	48	—	—
		Smolt	—	—	130154	38	63	—	37	—	—
Slaney, Berg & Tautz (1993)	<i>O. mykiss</i>	Smolts	Downstream	32 or 28	95258	Unknown (return figures based on downstream fisheries)		—	—	Release	Reach of release correlated to reach where adults were caught
				22 or 18	97051	Unknown (all other return figures based on downstream fisheries)		—	—	Release	—
				12 or 1	92282	Unknown (all other return figures based on downstream fisheries)		—	—	Release	—
Solazzi, Nickelson & Johnson (1991)	<i>O. kisutch</i>	Smolt	No transport	—	750798 (total)	1475	—	99.9	0.1	—	Smolts were transported downstream to lower Columbia River, estuary, or ocean. 'Rearing site' = Columbia River, 'Other Sites' = other river systems
			Downstream	205		29	—	96.6	3.4	—	—
			Downstream	232		49	—	95.9	4.1	—	—
			Estuary	253		66	—	93.9	6.1	—	—
			Ocean	253		100	—	79	21	—	—
			Ocean	272		48	—	62.5	37.5	—	—
Vreeland, Wähle & Arp (1975)	<i>O. kisutch</i>	Smolt	Downstream	223	100914	347	97	3	—	Release	—
Wagner (1969)	<i>O. mykiss</i>	Smolt	Downstream	50	81000	161	71	29	—	Release	—

Species: *Oncorhynchus kisutch*, coho salmon; *O. mykiss*, steelhead/rainbow trout; *O. tshawytscha*, Chinook salmon; *S. trutta*, brown trout; *Salvelinus alpinus*, Arctic char.
 PST, parr-smolt transformation.

Currently, there are few data on homestream fidelity of salmonids, as noted by Keefer & Caudill (2014) in their review on this topic. As a result, estimates of homestream fidelity among *Oncorhynchus* spp. are coarse, and the hypotheses proposed by Quinn (1984) remain largely untested. For example, the data currently available show similar homestream fidelity of pink and chum salmon (Keefer & Caudill, 2014), contrary to what we might expect. There are several factors that restrict our ability to measure homestream fidelity (Keefer & Caudill, 2014), such as the near-impossible task of monitoring all recipient non-natal sites, and quantitative estimates of fidelity may remain coarse for some time. Research that compares the responses (e.g. behavioural or physiological sensitivity) of different populations or species to migratory cues, however, could help determine the effects of the ecological factors on migratory behaviour, from which the relative degrees of homestream fidelity could be inferred.

(2) Effects of physiological and environmental factors on olfaction

There are various physiological and environmental factors that may affect the olfactory ability of migrating adults, and therefore their ability to locate spawning grounds, but there is little information currently available. Cortisol, for example, increases dramatically with maturation level during the spawning migration (Schmidt & Idler, 1962; Fagerlund, 1967) although its effects on olfaction are unknown. Carruth, Jones & Norris (2002) suggest that increased cortisol levels might improve the fish's ability to recall imprinted odours, just as chronic stress has been linked to increased long-term memory retention in mammals.

Thermal elevation in migratory rivers could also affect olfaction. Recent studies on Atlantic salmon (*Salmo salar*) have found that rates of straying increase with warmer temperatures (Valiente, Beall & Garcia-Vazquez, 2010; Horreo *et al.*, 2011). Keefer *et al.* (2008a) also observed unusually indirect homing behaviours amongst Chinook salmon (*Oncorhynchus tshawytscha*) that were correlated with increased water temperatures. It is possible that migrants depart from their normal migratory route to limit the physiological costs associated with warm migration temperatures (Martins *et al.*, 2012). It is also possible that temperature could affect the olfactory system, but this has not yet been distinguished from the possibility of thermoregulatory behaviours.

In addition to temperature and stress, CO₂ concentrations and pH levels may affect olfaction during the spawning migration. The olfactory response of salmonids is reduced at pH levels below 6.5 (Hara, 1976; Moore, 1994), and the behavioural response of juvenile Atlantic salmon (*Salmo salar*) to chemical alarm cues is temporarily reduced in slightly acidic streams (pH ~6) (Leduc *et al.*, 2010). The effects of low pH do

not appear to be permanent, although few studies have tested this. More subtle decreases in pH (or elevation in CO₂) – in the range of projected ocean acidification – impaired the ability of larval reef fish to select suitable settlement sites through olfactory cues (Munday *et al.*, 2014). The lasting effects of modest reductions in pH (that reflect projected ocean acidification) on the behavioural response of salmonids, lamprey, or other anadromous fish to migratory cues have not been tested. Ongoing ocean acidification and increases in oceanic CO₂ could cause olfactory impairment that, even if not permanent, could continue into part of the freshwater phase of the migration. Future studies that focus on the behavioural response of migrating adults following exposure to acidic or elevated CO₂ conditions will help determine whether future climate change might reduce navigation abilities during the spawning migration.

(3) Effects of toxicity on the spawning migration

Exposure to environmentally realistic concentrations of toxins interferes with the olfactory system in fish (Tierney *et al.*, 2010). However, as Tierney *et al.* (2010) note, studies that explore the effects of toxicity on the spawning migration of salmonids are limited (e.g. Saunders & Sprague, 1967; Scholz *et al.*, 2000), and there is a similar lack of information for lamprey (Tierney *et al.*, 2010). From a conservation perspective, pollution is perhaps the most critically understudied environmental factor affecting olfaction. Many major river systems that sustain large populations of anadromous fish contain large amounts of pollutants. In the Columbia River, for example, there are significant amounts of toxins such as polychlorinated biphenol, dichlorodiphenyltrichloroethane (DDT), and mercury, some of which are on the rise (Environmental Protection Agency, 2009). In highly polluted systems, which are also often home to declining fish populations, research that focuses on the impact of toxins on the olfactory system and behaviour of migrating fish will help define the severity of the threat that pollution poses.

(4) Olfactory navigation in non-salmonids

Of the suitable papers that we found, the majority are on Atlantic salmon (*Salmo salar*) and Pacific salmon (*Oncorhynchus* spp.) (Fig. 3). The family Salmonidae constitutes 88% of the papers, with the genus *Oncorhynchus* contributing 57%. Most of the non-salmonids studied are lamprey species, particularly sea lamprey (*Petromyzon marinus*). Being semelparous, the ability of most *Oncorhynchus* spp. to locate spawning grounds is under particularly strong selection pressure. Their high level of homing success suggests that these fish have evolved fine-tuned homing mechanisms that could make *Oncorhynchus* a model genus for olfactory navigation research. This does not, however, make

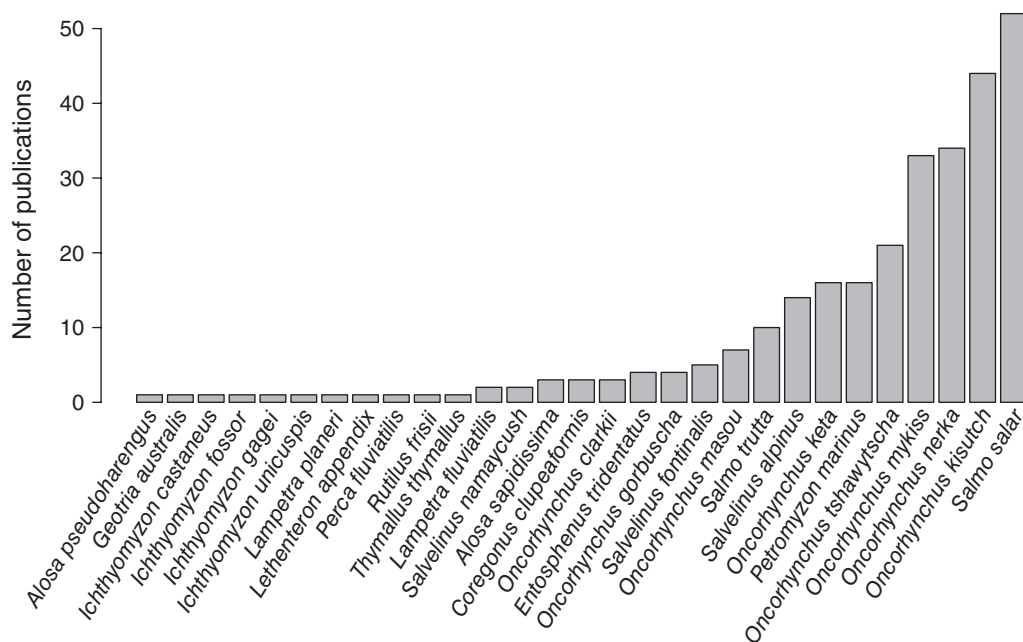


Fig. 3. Distribution of the number of peer-reviewed publications relating olfaction to the spawning migration in different species of anadromous fish.

them representative of all anadromous fish. Additionally, some of the species currently being overlooked are critically endangered (*e.g.* Atlantic sturgeon, *Acipenser oxyrinchus*). Given the direct influence of spawning site detection on reproductive success, conservation efforts for endangered species will benefit from a greater understanding of their navigation abilities.

There is also a strong bias towards hatchery populations in studies on salmon homing. Hatchery populations were used in 67% of the 224 relevant papers we found. Furthermore, of the studies focusing on wild populations of salmonids, only 44% used wild-born fish, while the rest used hatchery- or laboratory-reared offspring of wild populations. Hatchery-reared fish are suspected to differ from wild fish behaviourally and physiologically, and studies that use hatchery fish, such as imprinting experiments, have suggested that their unnatural rearing environment may affect the interpretation of their findings (Dittman & Quinn, 1996). With laboratory imprinting studies, for example, the introduction of novel water or odorants during developmentally relevant periods would more accurately reflect natural conditions, and may produce informative results. Also, most imprinting studies to date have focused on coho salmon (*Oncorhynchus kisutch*), which reside in fresh water for one or more years before migrating to the ocean. Research on species with different juvenile life histories, such as pink salmon (*O. gorbuscha*) or chum salmon (*O. tshawytscha*) that migrate directly to the ocean, may produce results that differ from those found with coho salmon.

(5) Identity and temporal consistency of candidate migratory cues

Several bile acids used by lampreys have been chemically identified, but the entire suite of directional cues has not yet been determined. Furthermore, the majority of lamprey research has focused on land-locked sea lamprey (*Petromyzon marinus*), and the chemical compounds have not been tested on many of the other lamprey species. In salmonids, meanwhile, migratory cues have not yet been conclusively identified. Recent studies on amino acids provide the first steps in identifying the chemicals that act as migratory cues (Ueda, 2011). One aspect in particular that has been missing from salmon homing research is consideration of changes in the concentrations of chemicals over time. In order for chemicals to act as migratory cues, their concentrations (or relative concentrations) during imprinting and during the spawning migration, which can occur many years apart, presumably must remain similar. For chemicals derived from conspecifics, this may not be necessary, so long as they are detectable. Chemicals that are derived from other organisms or organic material present in the natal water, however, may not remain consistent over time. Yamamoto, Shibata & Ueda (2013) measured the concentration of amino acids in natal water at 4-year intervals – first as juvenile chum salmon (*Oncorhynchus keta*) were migrating to the ocean (when imprinting may occur), and then during their return as adults. The composition of amino acids varied between these 4-year intervals, with approximately half the amino acids changing significantly in their relative concentrations. Mature adults, however, were equally attracted to

both types of artificial natal water (one containing the concentrations found during the outmigration and the other containing the concentrations found during the return migration). The attraction of mature adults to waters with differing compositions and/or concentrations of amino acids is not yet understood and should be explored further. Additional studies that take into account natural changes in relative concentrations of amino acids and other chemical groups over time will be critical to the identification of migratory chemical cues.

V. HIERARCHICAL NAVIGATION HYPOTHESIS: A NEW EXPLANATION OF NATAL HOMING IN SALMONIDS

Taken together, research to date on salmonids suggests there is a need for further studies of the relative importance of imprinted cues and conspecific cues. Natal homing in salmonids appears to involve an imprinting component (the Olfactory Imprinting Hypothesis), but there is also substantial evidence that suggests that migrating adults are attracted to conspecific cues (the Pheromone Hypothesis). While not mutually exclusive, the two hypotheses are often discussed as competing explanations of natal homing, with imprinting favoured over pheromones due to (i) the absence of juveniles in natal water during the spawning migration for some species, and (ii) the abundance of evidence of imprinting (Ueda, 2011; Keefer & Caudill, 2014).

Based on the research synthesized herein, the following points outline our current state of knowledge on natal homing in salmonids: (i) they are capable of imprinting to chemical compounds; (ii) these chemicals are presumably consistent in their concentration and/or composition over time, at least to the extent that adults can recognize water they imprinted on as juveniles; (iii) it is exceedingly unlikely that the homestream odours are detectable from the estuarine habitat, particularly for long-distance migrants; (iv) fish are capable of detecting conspecific cues, and there is evidence of population-level discrimination; and (v) other members of the same population (e.g. juveniles) are not always present in the homestream during the adult migration.

With these points in mind, we have developed a hypothesis, referred to here as the Hierarchical Navigation Hypothesis, which seeks to explain how salmonids locate spawning grounds. This hypothesis unifies the widely acknowledged olfactory imprinting and pheromone hypotheses, and incorporates suggestions first made by Quinn *et al.* (1983); Brannon & Quinn (1990) and Dittman *et al.* (2010). We propose that migrating adults rely on three tiers of directional cues in a hierarchical fashion (Fig. 4). Migrants first search for imprinted chemicals, which act as the primary directional cue. In the absence of imprinted cues, returning adults search for conspecific cues (or pheromones),

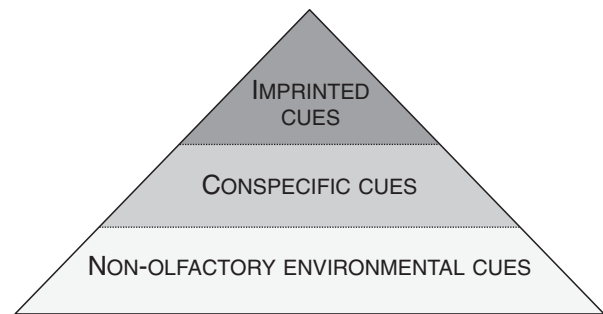


Fig. 4. The Hierarchical Navigation Hypothesis: a new explanation of the navigation process in salmonids migrating upstream. Migrants primarily rely on imprinted olfactory cues (likely to include a wide spectrum of odorants present in the natal tributary, which combine to form a unique chemical mixture), and secondarily on conspecific cues. In the absence of these, they move towards other environmental indicators, such as optimal temperature or flow.

which act as a secondary directional cue. If conspecific cues are also absent, they rely on other environmental indicators (such as flow, temperature, and substrate) that influence migratory conditions or spawning habitat. Such information would lead stray migrants to suitable non-natal spawning sites.

The imprinted cues likely include a wide spectrum of odorants present in the natal tributary, including conspecific cues, which combine to form a unique chemical mixture. We hypothesize that components of this imprinted mixture do not elicit an attractive response when disassociated from the other chemicals, with the exception of conspecific cues. Conspecific cues may therefore be incorporated in the primary tier of imprinted chemicals, but could also act as a secondary directional cue, in which they elicit an attractive response independently (e.g. when migrants have strayed away from the imprinted mixture), and without the necessity of imprinting. It is possible that within this secondary tier exists two levels, the first being cues from their own population, which would lead migrants to natal water, and the second being cues from other populations, which would lead them to non-natal habitat.

This hypothesis may be applied to previous research. First, there is evidence that adult migrants will select imprinted cues over pheromones when exposed to both. For example, Brannon & Quinn (1990) demonstrated that adult coho salmon (*Oncorhynchus kisutch*) will migrate directly past conspecifics and continue upstream to water they have imprinted on. Similarly, when adult Arctic char (*Salvelinus alpinus*) were taken out of their natal river and held in a nearby tributary, none of the other migrants were attracted into the nearby tributary, despite migrating directly past its outflow (Black & Dempson, 1986). Furthermore, when given the choice between natal water and foreign water that contains juveniles of their own population, adult coho salmon show a significant preference for the natal

water (Brannon, Whitman & Quinn, 1984). Although the number of studies that have directly tested the relative preferences of imprinted and conspecific cues is limited, they all suggest that imprinted cues are more attractive, and there is currently no evidence that indicates a preference in the opposite direction.

In the absence of any imprinted cues, such as when migrants have strayed from their normal route, salmonids migrate towards their conspecifics. Nordeng (1971, 2009), who first proposed the Pheromone Hypothesis, demonstrated this in Arctic char (*Salvelinus alpinus*). Juveniles were reared at a satellite location, with no opportunity to imprint on natural streams, and adults subsequently returned to the waters containing juveniles from their own population. In another study, Quinn, Brannon & Dittman (1989) released two groups of coho salmon (*Oncorhynchus kisutch*) smolts roughly 40 and 18 km downstream from their rearing sites. The majority of coho returned to a hatchery a few kilometres upstream from the release site, despite (i) being transported well after the PST (and therefore presumably after imprinting occurred), and (ii) never having experienced the water at that hatchery. As the authors suggest, the imprinted cues of the rearing sites were potentially out of detection range from the downstream location (both rearing sites are heavily diluted in Lake Washington before reaching the release site), and transportation prevented any opportunity for sequential imprinting. As a result, the migrants were instead attracted to conspecifics at the hatchery. Furthermore, the migrants did not return to an equally proximate hatchery that contained very few adult coho salmon (fewer than 1% of the number at the other hatchery), which suggests the migrants were attracted to the strong concentration of conspecific cues, and not a different hatchery-related cue. Dittman *et al.* (2010) conducted a study in which Chinook salmon (*O. tshawytscha*)

smolts were transported and released before their outmigration. The majority of returning adults that strayed from their release site entered rivers that were home to wild populations of conspecifics, especially when they had strayed a large distance (>25 km). A similar result, in which the majority of strays enter rivers with populations of conspecifics, has been found in Atlantic salmon (*Salmo salar*; Jonsson, Jonsson & Hansen, 2003). There is also evidence that stocking a fishless river with Atlantic salmon attracts stray adults from other populations (White, 1934; Solomon, 1973).

Johannesson (1987) observed spawning migration behaviour of Atlantic salmon that further supports the notion that migrants will return primarily to imprinted cues and secondarily to pheromones. Smolts were released in a harbour, and they returned as adults to the release point. The adults remained in this area until a new group of smolts were placed in pens in an experimental pool that empties into the harbour, after which point the adults swam into the experimental pool. The experiment was repeated multiple times, and the same result – adults remaining in the harbour until smolts were added into the pool – was achieved each time. While the author noted that the findings appear to simultaneously support and contradict the pheromone hypothesis, they are more comprehensible when viewed in the context of hierarchical navigation: the adults first returned to imprinted cues (the harbour), then towards conspecifics (the experimental pool).

In addition to published research, there is anecdotal evidence that salmonids migrate towards conspecifics in the absence of imprinted cues. In the summer of 2012, as part of an unrelated experiment, we held 20 sockeye salmon (*Oncorhynchus nerka*), in Cayoosh Creek (British Columbia, Canada), a tributary of the Seton River, which itself is a tributary of the Fraser River (Fig. 5). Cayoosh Creek does not contain any salmon populations

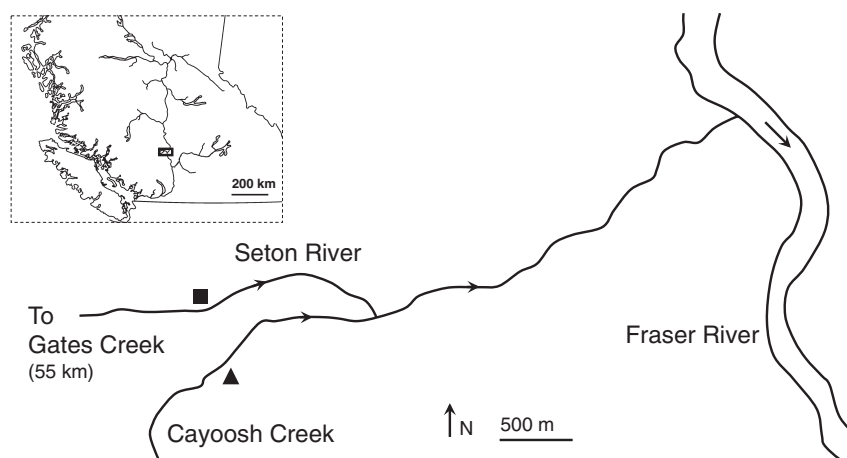


Fig. 5. Map of the area in the Fraser River system of British Columbia, Canada (inset) where anecdotal evidence suggests that migrating salmon are attracted to conspecifics in the absence of imprinted cues. Sockeye salmon were captured in the Seton River (square symbol) during their upstream migration to Gates Creek, and held overnight in Cayoosh Creek (triangle symbol), a non-salmon-bearing stream.

and sockeye salmon are not transiently found there. The Seton River is part of the migratory route for Gates Creek sockeye, but not for other populations. Within 12 h of placing the sockeye salmon in Cayoosh Creek, more than 50 free-swimming sockeye were observed alongside and directly downstream from those being held. DNA samples were collected from four of the free-swimming fish, and they were all identified as stray sockeye, originating from two non-Gates-Creek populations. Since sockeye salmon do not occur in Cayoosh Creek under normal circumstances, these stray salmon may have been attracted to the odours of co-migrating adults that had been placed there for experimental purposes. That each of the salmon were identified as strays further suggests that salmon might migrate towards conspecifics specifically in the absence of imprinted cues.

If neither conspecifics nor imprinted cues are present, other environmental characteristics may become directional cues indicating suitable non-natal spawning habitat. There are a variety of non-olfactory environmental properties that might act as directional cues to stray migrants, such as discharge, temperature, and oxygen levels (Keefer & Caudill, 2014). Higher flows, for example, can be attractive: in a study on Chinook salmon (*Oncorhynchus tshawytscha*) in New Zealand, there was a positive relationship between the number of strays in a given river and its discharge (Unwin & Quinn, 1993). Migrating adult salmon utilize thermal refugia to conserve energy as they swim upstream (Mathes *et al.*, 2010), and stray migrants in high temperatures may be attracted to waters closer to their optimal temperature. There are other environmental factors, such as substrate, cover, stream width, and gradient, that can affect spawning site selection and the spatial distribution of spawners (Cram *et al.*, 2013). Non-olfactory environmental characteristics might also be used as a supplement to primary or secondary cues. For example, adult migrants entering a main stem river may not always need to rely on a complex system of sequentially imprinted waypoints, but might rather simply remain in the high discharge until they are within close enough proximity to detect their natal tributary. There is very little information on the attractiveness of non-olfactory environmental characteristics to stray migrants, however, and their potential role as tertiary directional cues has not been tested. Research in this area is therefore needed before this portion of the Hierarchical Navigation Hypothesis can be supported or challenged.

From an evolutionary standpoint, this method of homing could be adaptive. For adults that have strayed from their normal migratory route, movement towards conspecifics would increase the probability of locating suitable non-natal spawning habitat, as well as potential mates, and therefore increase fitness. Such an attraction can also encourage genetic mixing between populations, which can help reduce inbreeding depression (Hendry *et al.*, 2004). When neither imprinted nor

conspecific cues are present, an attraction to environmental characteristics that are indicative of high-quality spawning habitat would maximize reproductive success and offspring survival in unoccupied waters. Similarly, when imprinted and/or conspecific cues are present at peak concentrations, such as on spawning grounds, an attraction to favourable environmental characteristics will optimize reproductive success and offspring survival within that area. Furthermore, an attraction to uninhabited but environmentally suitable spawning grounds increases the probability of successful colonization, which could in part explain instances of rapid colonization such as in pink salmon (*O. gorbuscha*; Pess *et al.*, 2012).

Future research can help test the Hierarchical Navigation Hypothesis further. As seen in Table 4, numerous studies have documented the olfactory sensitivity of salmonids to specific chemical compounds, any of which may guide migrating adults. In order to provide evidence for or against this or other natal homing hypotheses, studies will need to simultaneously incorporate various chemicals to determine their relative importance as migratory cues. Furthermore, while the commonly used electrophysiological approaches provide an estimate of basic sensitivity to individual chemicals, they do not demonstrate a behavioural response. To determine whether a chemical is acting as a migratory cue, the behaviour of the fish in response to the chemical must therefore be analysed. As such, research that integrates different chemicals and assesses direct behavioural responses to these chemicals will test the homing hypotheses most effectively.

VI. CONCLUSIONS

(1) Several decades of research have provided strong evidence that many anadromous fish rely primarily on olfaction to locate their spawning grounds during the freshwater phase of the spawning migration. In this review we focused on two types of spawning migrations, ‘natal homing’ (migration to natal water to spawn) and ‘non-specific homing’ (migration to the general geographic area of birth, but not necessarily natal water), and olfaction is important for both. Salmonids and lamprey have been the most extensively studied groups of species for each of these two migration types, respectively, and have provided the basis for our understanding of how olfaction directs adult migrants.

(2) The behavioural and physiological responses of lamprey and salmonids to various odours have been studied extensively. In general, these fish respond to amino acids, bile acids, salts, metals, prostaglandins, and other hormones, and the responses occur at concentrations that are relevant to natural freshwater conditions. Additionally, the ability of natal homing species to imprint on odours as juveniles has been

conclusively demonstrated. Juveniles that are exposed to a unique odorant, particularly during the parr–smolt transformation stage, display an attractive response to the odorant as migrating adults. The recent introduction of molecular and genetic analyses in olfactory research has provided new directions for exploration and our first glimpse of the molecular processes that drive the olfactory system in anadromous fish.

(3) Our synthesis also highlights limitations in past research and we have identified knowledge gaps that warrant investigation. These gaps include the potential effects of various environmental factors on the olfactory response of migrating adults. The effects of some factors, such as toxins and stressors (e.g. high temperatures, acidity), may have significant conservation and management implications, as the ability to locate spawning grounds successfully is critical to reproductive success. In addition, variation in the olfactory responses of different species or populations of salmonids has rarely been studied directly. Combining such information with variation in life histories, such as the juvenile rearing stages, will help elucidate the role of olfaction during the spawning migration, and could also have implications with respect to the evolutionary history of olfactory sensitivity to spawning grounds. Our review also highlights biases in focal species within this field of research. The majority of research has focused on salmonids, particularly those from hatchery populations, while little attention has been given to other species of anadromous fish, some of which are threatened or endangered.

(4) There are two hypotheses that currently dominate the field of natal homing in salmonids: the Olfactory Imprinting Hypothesis (or its modified form – sequential imprinting) and the Pheromone Hypothesis. There has been evidence to support each of these, and they are often introduced as competing explanations for natal homing (e.g. Ueda, 2011; Keefer & Caudill, 2014). We have proposed an alternative explanation, the Hierarchical Navigation Hypothesis, which unifies and expands upon the two predominant hypotheses. The hypothesis posits that migrating adults respond to different cues in a hierarchical fashion. Imprinted odours, which are unique in composition and may be derived from many different components of the natal tributary, provide the primary directional cue. Conspecific odours provide a secondary directional cue, and may be particularly attractive to strays that are not able to detect imprinted cues. Non-olfactory environmental indicators, such as substrate or discharge, may act as tertiary cues and assist strays in finding suitable non-natal spawning habitat.

(5) While past studies have incidentally lent evidence that supports the Hierarchical Navigation Hypothesis, we have provided examples of future directions for research that can further test this hypothesis. This includes a movement away from the odorant-specific experiments that have been favoured in previous

research, towards an integrated approach that assesses relative responses to different odours. Furthermore, while many studies have examined the electrophysiological responses of salmon, and more recently the molecular or genetic responses, these approaches only highlight responsiveness or sensitivity to chemical cues. In order to determine behavioural responses, some form of behavioural assay is necessary.

VII. ACKNOWLEDGEMENTS

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